

HYDROBIOLOGIA

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Investigations into the Ecology of Polluted Inland Waters in the Transvaal¹⁾

Part I

by

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¹⁾ Being in part fulfillment of the requirements for the degree of Doctor of Philosophy, University of Cape Town, 1960.

Part I

The Physical, Chemical and Biological Conditions in the Jukskei-Crocodile River System

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I. INTRODUCTION

In South Africa there has been an increased interest in the problems connected with the disposal of effluents, especially those from the heavily industrialized Witwatersrand which is one of the principal watersheds of the country. In an early unpublished report STANDER drew attention to bacterial contamination of rivers and the resulting process of self-purification. Although no specific reference was made to South African conditions, the report stressed the necessity for proper investigations to be carried out in South Africa. WILSON & RAPSON (1949) further emphasised the need of research and advisory facilities for effluent disposal and treatment, and pointed out that although many organisations existed in South Africa which controlled one or other aspect of water conservation and usage, there was as yet no unifying authority. They also pointed out the necessity of regional planning of water supply and use, and they emphasised that this was of paramount importance in view of the country's limited water resources. They drew attention to the fact that in Britain, Germany and in the United States of America, river basins and catchment areas are recognised as units, in which there can be effective control of pollution and practice of conservation.

STANDER (1950) brought the problem of water pollution nearer to the door of industry, and pointed out the problems which resulted from industrial pollution of the country's water supply. The same author in 1951, in an endeavour to implement his previous remarks, presented a programme for the complete investigation of the Vaal River Basin, which could fairly easily be adapted for other important river basins in the Republic of South Africa.

In a further series of publications, STANDER (1951 and 1952) emphasised the need for the reclamation of sewage and industrial effluents for re-use. He pointed out that 75% of the total water consumption (domestic and industrial) by municipalities of the Witwatersrand reached the various sewage disposal plants. The effluent from these plants was an immediately available source of raw water supply, but usually it was disposed of uneconomically by irrigation on sewage farms.

The repeated warnings given by these and other authors on the doubtful future of South Africa's water resources, if pollution were not controlled by legislature, initiated in 1955 the Water Act of the Government. This Act gives the Minister of Water Affairs con-

siderable power in the prevention of pollution of the inland and coastal waters. However, the implementation of the Act had to be based at all times upon fundamental and applied research into river and lake pollution, and so there followed an increase in active research into the problem in South Africa.

HARRISON & ELSWORTH's work on the Great Berg River in the Western Cape (1958), a direct result of the decisions taken at the African Regional Scientific Conference held in Johannesburg in 1949, was in its main outline purely hydrobiological, and as these authors point out it was of the utmost importance to investigate the biology of a clean river system before trying to evaluate the results of surveys carried out on polluted streams. HARRISON's (1958b) work on polluted streams, together with the main work on this river, provided a very satisfactory pattern upon which further research could be based. A hydrobiological study of the Tugela River in Natal followed shortly afterwards (OLIFF 1960). This work was modelled on lines similar to the survey described by HARRISON & ELSWORTH (1958) since apart from the main study it also included an investigation of a polluted tributary. However, these two systems were not severely polluted, although threatened by expansion in industry and urbanisation. In view of the Water Act of 1955 a study of a seriously polluted system, with a comparatively small flow and ending in an irrigation dam, was of immediate importance. The streams flowing from the Witwatersrand in the Transvaal were ideally situated for this study since they were nearly all polluted from their source, which placed a heavy load on their self-purifying potential, and on both the southern and northern slopes of the Witwatersrand the streams entered large irrigation dams.

In 1955 the Transvaal Provincial Administration and the South African Council for Scientific and Industrial Research established a research fellowship for the study of the pollution of the Jukskei-Crocodile River system, which rises in Johannesburg, the population and industrial centre of the Witwatersrand, and which flows into Hartbeespoort Dam, an important irrigation dam 52 miles north of Johannesburg.

A Steering Committee was appointed by the South African Council for Scientific and Industrial Research to guide the research work and present objectives for the study. The members of the Committee were as follows:

Dr. W. S. RAPSON Vice President, S.A.C.S.I.R.

Dr. G. J. STANDER Director, National Institute for Water Research.

Mr. T. J. STEYN Director, Department of Nature Conservation, Transvaal Provincial Administration.

Mr. S. S. DU PLESSIS Senior Fisheries Officer, Department of Nature Conservation, Transvaal Provincial Administration.

Dr. A. D. HARRISON Principal Research Officer, S.A.C.S.I.R.

Dr. B. R. ALLANSON Transvaal River Research Fellow.

The objectives laid down by the Committee were:

1. The determination of the present chemical and biological conditions of the streams forming the Jukskei-Crocodile River system.
2. The determination of sources of pollution of the system and the effects of these pollutants on the biological conditions of the system.
3. The formulation of biological indices of pollution. In addition such a study would extend the work of HARRISON (1958) and OLIFF (1960) on the zoogeography of known genera and species of freshwater animals in South Africa as well as accentuating a different aspect of freshwater ecology. New species have been described or are being described by specialists.

Apart from biological and chemical studies, bacteriological and algal (diatom) studies have also been carried out. The diatom studies have been published (CHOLNOKY 1958) as well as the results of the bacteriological studies (KELLER 1960).

The first part of this paper presents the results of, and conclusions based upon a study of unpolluted and polluted streams within the same river system. The second part describes the results of a brief but cogent limnological survey of Hartbeespoort Dam into which both polluted and unpolluted streams flow.

The objectives laid down by the Steering Committee have been achieved as far as possible. However, no attempt has been made to describe indicator species as it was soon apparent that no useful information would be gained by this. Far more valuable information for a re-appraisal of saprobic states was obtained by the analysis of data from the chemical and biological studies, using association of species, and from the diatom and bacteriological studies.

Previous ecological studies have made use of log-normality to describe the population characteristics of closely allied species, e.g. of diatoms, macrolepidoptera and birds. In this study the same procedure has been used to describe relative abundance of species in the heterogenous invertebrate populations of the habitats examined.

What is pollution?

KLEIN in his excellent book, "Aspects of River Pollution" (1957), defines pollution as "anything causing or inducing objectionable conditions in any water course and affecting adversely any use, or uses to which the water thereof may be put".

There is certainly nothing to be gained by analytical comment on this definition and for the purposes of this paper it is accepted as a reasonable statement of fact.

If pollution, as defined above, is being interpreted through its effects on particularly the invertebrate fauna and flora of a stream, it is equally convenient to accept HAWKE's definition given in his chapter of the above work. He states: "Pollution may be said to occur when the discharge of a substance into a stream alters appreciably the composition or distribution of ... communities ...". This definition is dependent upon the view that the nature of animal and plant communities in a stream is mainly determined by three interrelated factors: (i) physical and chemical nature of the water; (ii) nature of the stream bed; (iii) current speed; and that the discharge of substances into the stream acts by changing any one of these factors.

II. GENERAL DESCRIPTION OF AREA AND RIVER SYSTEM

1. Topography

The "Highveld" is a grassland region, lying at a considerable altitude, which occupies the greater part of the Transvaal and the Orange Free State. In the Transvaal it is traversed by one of the most important watersheds in the Republic of South Africa, the Witwatersrand, which divides the Limpopo River basin to the north from the Vaal River basin to the south. This watershed is the most heavily industrialised and therefore densely populated region south of the Sahara, and the headwater streams flowing northwards and southwards carry a large portion of the industrial and domestic wastes. The north-flowing Jukskei-Crocodile River system receives a considerable amount of these wastes as it rises in Johannesburg and its environs.

The catchment area of the Jukskei-Crocodile River system occupies 970 square miles to the north of the Witwatersrand and lies at an altitude of between 6000 and 4000 feet. Johannesburg and Krugersdorp are the south-eastern and south-western limits of the area. Climatically the region is harsh in winter, cold and mainly dry with occasional snow on the Witwatersrand. The summer is warm to hot

TABLE 1
THE PHYSICAL AND CHEMICAL CONDITION OF
THE BOTTOM SEDIMENTS OF HARTBEESPOORT DAM

| Averages | Station 1 | Station 2 | Station 3 |
|---|------------------------|----------------------|----------------------|
| Particle size | 10.6 μ (ca. 43.5%) | 11.5 μ (ca. 55%) | 19.5 μ (ca. 75%) |
| Total C | 1.125% | 1.311% | 1.946% |
| Total N | 0.167% | 0.198% | 0.216% |
| Total Fe | 4.234% | 4.334% | 2.997% |
| Total PO ₄
HCl soluble | 0.112% | 0.096% | 0.184% |
| Total Cu in ppm.
(mg/Kg Dry Mud
at 105°C) | 65.5 | 60 | 58.5 |

SULPHIDES:

| | | | |
|---|-----------|-----------|-----------|
| as S in ppm.
mg/Kg Dry Mud
at 105°C | Station 1 | Station 2 | Station 3 |
| Winter | 132 | 113 | 75 |
| Summer | 241 | 240 | 103 |

FERROUS IRON:

| | | | |
|--------|-----------|-----------|-----------|
| | Station 1 | Station 2 | Station 3 |
| Winter | 34.3% | 33% | 35.2% |
| Summer | 45.5% | 42% | 44.7% |

THE COMMON SPECIES IN THE MARGINAL VEGETATION AT STATION 23,
MEERHOF, HARTBESPOORT DAM

* The relative incidence as % is given below each number : The Entomostracan component is calculated separately.

[illegible]

and throughout the region 85—90 % of the rain falls in the six summer months, i.e. between November and April. Table 1 is taken from National Resources Development Council Report (1957).

The vegetation covering the catchment area is divided into three types: —

- (i) Highveld, composed of grassy plains
- (ii) Bankenveld, where the grass-plains are broken up into parallel grass covered ridges
- (iii) Mixed bushveld, found in the vicinity of Hartbeespoort Dam.

The streams flow northwards and unite before opening into the Hartbeespoort Dam as the Crocodile River. The headwaters of the river system are divided into two sub-systems: the Crocodile River and its major tributary, the Blaauwbank stream, which drain the western Witwatersrand and are unpolluted; and the polluted Jukskei River with its unpolluted tributary the Klein Jukskei stream and two polluted tributaries, the Sandfontein and Braamfontein, which drain the north-western Witwatersrand. (Figure 1).

The Jukskei River rises in Bezuidenhout Valley, now a suburb of Johannesburg. At Buccleugh, 13 miles from its source, the river receives the Modderfontein stream. At Leeuwkop Prison Farm 7 miles lower down, the Jukskei River receives the Sandfontein and Braamfontein streams which rise in the northern residential zone of Johannesburg. Seven miles downstream of this point at the Krugersdorp road bridge the river receives its only unpolluted tributary, the Klein Jukskei stream. Between this point and the confluence with the Hennops River, the river flows for a distance of 15 miles. About halfway between these two points the Jukskei River joins the Crocodile River. This confluence was inaccessible for sampling purposes. Eight miles below the confluence with the Hennops River the Crocodile River flows into Hartbeespoort Dam. The Jukskei River before and after confluence with the Crocodile River is referred to as the "Main Stream" and its profile is shown in Figure 2. The total distance followed by the main stream until it enters Hartbeespoort Dam is 62 miles, and over this distance the stream drops 1500 feet. The sampling stations, their siting and habitats sampled are given in Table 2 and a number of the more important are shown in Plates I, II, III and IV.

2. Geology

The Witwatersrand is built up (DU TOIT 1954) of white quartzites, conglomerates and shales belonging to the upper and lower Witwatersrand system, all sedimentary rocks. Igneous rocks are repre-

sented by Ventersdorp lavas, made up of amygdaloidal diabase and are especially common in Bezuidenhout Valley, the source zone of the Jukskei River, which before urbanisation was largely swampy.

Immediately to the north of the Witwatersrand is a denuded granite dome lying between Johannesburg and Pretoria. This dome forms undulating country with fairly deep valleys along which run the rivers and streams, the subject of this investigation. The northern edge is bounded by a belt of dolomite through which the Crocodile River passes before cutting through the quartzites, shales and diabase of the Pretoria series, represented most obviously by the Daspoort and Magaliesberg ranges. KYNASTON (1907) notes that the courses of rivers in many parts of South Africa are unaffected by "prominent surface features such as hills and mountain ranges" but cut their way through, forming narrow gaps or "poorts". In the Pretoria series there are three such poorts which have been cut by the Crocodile River and it is at the most northerly poort that the Hartbeespoort Dam is built.

The soils covering the greater part of the catchment area are derived from old granite, and according to DU TOIT (1954) such soils are sandy. The southern part of the catchment area is heavily populated and bad farming practices in the rural areas apparently result in large sand and grit loading of the river water during flood periods, amply confirmed by the existence of a sand pumping plant on the banks of the Crocodile River at Station 21 below the entry of the Hennops River which removes large quantities of sand from the bed of the river.

3. Zonation and bottom characteristics of the main stream

HARRISON & ELSWORTH (1958) zoned the Great Berg River on the basis of profile steepness and the type of bottom. The Jukskei-Crocodile River system has a relatively shallow profile, and only one of the Berg River zones is present throughout the whole of the river: namely the *Foothill Stony run zone*. In the Berg River, HARRISON & ELSWORTH (1958) divided this zone into two parts. In Zone IIIa, the river dropped about 500 feet in four miles; the bottom was composed of clean stones and pebbles, and the pools were floored with quartzitic sand. In Zone IIIb the river dropped about 200 feet in 25 miles, and although the bed was still broken up into stony runs and large pools, the hard bottom was usually covered with silt. HARRISON & ELSWORTH noted that it was in this sub-zone that the river passed through farm lands.

In the main stream of the Jukskei-Crocodile River system the drop

s intermediate between those of IIIa and IIIb, being about 500 feet in 17 miles. However, the stony runs and pool stretches are silted up with coarse quartzitic sands, and nearer to Hartbeespoort Dam the long pool stretches are floored with a deep layer of fine mud.

The stream is then defined as an extended hard bottom stony run zone of the lower foothill type.

DE MEILLON, FRANK & ALLANSON (1958) reported that the Jukskei-Crocodile River system was similar to HARRISON's Zone IV: Foothill, Soft Bottom Zone. In view of the characteristics described here, this system should have been defined as above.

On the Highveld this type of river bottom is found over considerable distances, and as a mountain source zone is missing it is the only zone present until a river falls towards its soft bottom and flood plain zones. All rivers rising on the Highveld of the Republic of South Africa have this type of bed: the two largest are the Vaal River, flowing into the Atlantic Ocean, and the Limpopo River, flowing into the Indian Ocean.

HARRISON & ELSWORTH (1958) noted that the stony runs in the Berg River were mainly floored with round river stones, derived from Table Mountain sandstones, or quartzitic pebbles. In the Jukskei-Crocodile River system the majority of the stony runs were composed of granite slopes or boulders. However, where the Crocodile River breaks through the Pretoria and Daspoort hills the stony runs were floored with some quartzitic pebbles as well as shale slates. It has been difficult to zone the river system any further on physiographic characters. For the sake of convenience, however, the river system has been divided into Reaches by contour lines, taking the distance the river flowed between each 500 foot contour as the length of each Reach. This means that in the main stream, i.e. the Jukskei River both before and after it joins with the Crocodile River, there are three Reaches before the river flows into Hartbeespoort Dam.

These three Reaches have been called Upper, Middle and Lower.

Upper Reach — from 5,300—4,800 ft. contours

Middle Reach — from 4,800—4,300 ft. contours

Lower Reach — from 4,300—3,800 ft. contours

The Upper Reach extends from the source of the Jukskei River in Bezuidenhout Valley to just above Station 8 at the confluence of the Modderfontein stream with the Jukskei River.

The Middle Reach extends from this confluence to Station 20a at the confluence of the Jukskei River with the Klein Jukskei.

The Lower Reach extends from Station 20a to the entry into Hartbeespoort Dam at Station 22.

The tributaries of the main stream have been similarly classified. The Sandfontein and Braamfontein streams are classed as Upper

Reach streams, while the unpolluted Klein Jukskei River and the Crocodile River, the greatest source of unpolluted water, are classed as Middle Reach streams. All these streams have hard bottoms.

4. Water types and habitats

HARRISON & ELSWORTH (1958) made use of ALLEN'S (1951) divisions and definitions of water types found in a river. In the Jukskei-Crocodile River system only four types exist: pools, stickles, cascades and flats.

Within these water types varied habitats are found. In the Jukskei-Crocodile River system the following habitats have been sampled:

| | |
|---------------------|--|
| stony bottoms | — in stickles and cascades |
| sandy bottoms | — pools and flats |
| muddy bottoms | — pools |
| marginal vegetation | — covering the banks of pools, flats and stickles. |

III. SOURCES OF POLLUTION

Three main types of pollution have been encountered in this survey: sewage, mineral and incidental.

1. Sewage Pollution

(i) Bruma Sewage Works is situated between Stations 1 and 2 on the Jukskei River and serves the north-eastern suburbs of Johannesburg.

(ii) Cydna Sewage Works is situated between Stations 16 and 14 on the Sandfontein stream and serves the northern suburbs of Johannesburg.

(iii) Delta Sewage Works is situated between Stations 10 and 11 on the Braamfontein stream and serves the north-western suburbs of Johannesburg. Together these three sewage disposal plants discharged approximately 11,000,000 gallons of sewage effluent per day into the Jukskei River and the Sandfontein and Braamfontein streams.

The Chemical composition of the effluents from Delta, Cydna and Bruma Works

In Table 3 the average chemical composition of various effluents from the three main northern sewage works, which were either directly liberated into the headwater streams of the river system or irrigated in the vicinity of the river, are given for the years July 1956 to June 1957 and July 1957 to June 1958. At the Bruma and Cydna Works only a small proportion of the humus tank effluent passed

through filter beds while at Delta no provisions for such treatment were available and the Braamfontein stream received only primary effluent. During the tenure of this study all the works were overloaded at times of heavy rain. As a result these figures must be considered as a rather optimistic estimate of what was actually discharged into the streams.

2. Mineral pollution

There was only one main source of chemical factory effluent. This effluent arose primarily from the manufacture of dynamite but further contributions came from byproduct manufacture. The effluent from this factory flowed down the Modderfontein stream which joined the Jukskei River at Station 8. An indication of the quality of this effluent may be obtained from the analyses given for Station 7 on the Modderfontein stream in Table 4.

3. Incidental pollution

Incidental pollution of the Jukskei River and tributaries was of five types:

(i) Indiscriminate discharge of laundry and dry cleaning effluent coupled with highly polluting substances carried by storm water drains during heavy rain, from densely built-up areas such as Bezuidenhout Valley. The conditions at Station 1 near the source of the river reflected this situation quite well.

(ii) A poorly designed and very badly controlled compost installation at Station 5 which attempted to convert "night soil" from the nearby native location of Alexandra Township into stable compost. During the rainy season particularly, the seepage from this installation had a most deleterious effect upon the Jukskei River.

(iii) Intensive farming at the Leeuwkop Farm at the confluence of the sewage streams with the Jukskei River (Stations 9a, 9b and 9c). A considerable quantity of wet compost produced from pigsty wastes was used throughout the year.

(iv) The random defecatory habits of the rural Africans. The only noticeable effect on the Klein Jukskei River was bacteriological (KELLER 1960).

(v) The wash water from temporary sand washing plants which were moved from one point of the Jukskei River to another.

Pollution types, i—iii, occurred mainly in the summer, rainy season and, without special facilities which were not available, it was not possible to obtain reliable information on their chemical composition and rate of discharge. However, the effect upon the chemistry

of the river water was always clearly seen and measured (see pages 21, 22, 23, 25).

IV. METHODS

This study was planned and conducted by one water biologist who also acted as nominal head of the research team engaged in evaluating the bacteriological and algal (diatom) communities in the river system during the investigation.

Although the chemical part of this survey was at all times the responsibility of the author, analysis of the water samples was carried out by analysts of the National Institute for Water Research and specific acknowledgements are made in section XVI. The collection and analysis of the biological samples was carried out by the author.

During the period of the survey, November 1955 to February 1959, 430 water samples and 590 biological samples were collected and analysed. An estimated 300,000 animals were collected and sorted to species wherever possible.

1. Physical

Flow - weirs were constructed at two points in the system, and four gauge plates were erected at existing irrigation weirs by the Division of Hydrology, Department of Water Affairs, Pretoria. The total flow of the Jukskei-Crocodile River system was measured at a self-recording weir between Stations 21 and 22. The remaining weirs were read daily by observers.

Current speed was determined by a Stevens Midget current meter during the first year of study, and during the second year of work the measurements were repeated with a Ott "Lab. Minor" current meter.

Temperature was measured by a conventional -10° — 110°C "Emil" linear thermometer.

2. Chemical

The chemical methods employed were those normally accepted in water and sewage purification practice. Some analytical methods were improved, or discarded in favour of more accurate methods that appeared in current literature. Of particular note is the work of J. M. T. M. GIESKES (in press) on the determination of dissolved oxygen by a modification of the "OHLE (1953) Method".

References to the analytical methods used in this work are given at the end of this section.

Water samples were collected from the various river stations in

ark Winchester bottles. Wherever possible, samples were taken from the middle of the stream after the bottles had been rinsed three times with river water. It was usually unnecessary to increase the concentration of dissolved substances by evaporation in the laboratory and analysis was carried out directly upon filtered aliquots. All chemical samples collected were what are generally called snap samples. It was not possible to work on composite samples collected over 24 hours, and diurnal work was limited to the determination of changes in dissolved oxygen, pH and phosphate concentration. These were of immediate importance and could be carried out with the laboratory facilities available.

Analytical Methods Employed

| Analyses | Method References |
|----------------------------------|--|
| Free and Saline ammonia nitrogen | Standard methods for the examination of water, sewage and industrial wastes. 10th Edition 1955. American Publ. Health Association, New York. |
| Nitrate nitrogen | TARAS, M. J. (1950) Phenoldisulphonic acid method of determining nitrate in water. <i>Anal. Chem.</i> 22, 1020. |
| Nitrite nitrogen | HELLIGE: Procedure of GRIESS, ILLOSVAY. |
| Oxygen absorption (4 hour) | Standard methods for the examination of water, sewage and industrial wastes. |
| Chemical oxygen demand | Standard methods for the examination of water, sewage and industrial wastes. |
| Turbidity | HELLIGE: procedure turbidometry. |
| Dissolved oxygen | Standard methods for the examination of water, sewage and industrial wastes. RIDEAL-STEWART modification of WINKLER method and also a modification of OHLE's (1953) iodone difference method (GIESKES in preparation). |
| Chloride | Standard methods for the examination of water, sewage and industrial wastes. Method of MOHR, p. 60. |
| Carbonate | Standard methods for the examination of water, sewage and industrial wastes. |
| Alkalinity | Turbidometry. |
| Sulphate | Standard methods for the examination of water, sewage and industrial wastes. EDTA titration method p. 112. |
| Total Hardness | — ditto — |
| Calcium | — ditto — |
| Magnesium | HELLIGE Silica — molybdate procedure. |
| Silica | Standard methods for the examination of water, sewage and industrial wastes — gravimetric procedure. |
| Iron and Aluminium | Flame photometry. |
| Sodium { | Standard methods for examination of water, sewage and industrial wastes, p. 169.
Method C. |
| Potassium } | |
| Phosphate | |

3. Biological

(i) Apparatus and methods used for collection of field samples:

Conventional hydrobiological apparatus was used. All the sampling nets used were made from bolting silk of 23 meshes per centimetre (58 mesh' per inch).

The marginal vegetation was sampled with a hand net with a circular brass frame of 10" diameter x 1" depth attached to a stout wooden handle. The net was swept vigorously through the vegetation for a distance of between 10' and 15', depending upon the extent of the vegetation.

The stones in current (stickles and cascades) were sampled by a Surber sampler, one square foot in area. GAUFIN et al (1956) and particularly NEEDHAM & USINGER (1956) have adequately dealt with the limitations of this sampler. In view of this work, only one Surber sample was taken where stickles were limited in extent, and inspection indicated that little change could be expected in faunal composition across the stickle; but two or three were taken where the make-up of the stickles varied.

Bottom muds and sands were sampled by a scoop or shovel designed by the author. The LENZ Modification of the BIRGE-EKMAN grab as used by HARRISON and ELSWORTH in the survey of the Great Berg River was not used because the sediments were unsuitable. In the muddy sediments there was so much coarse plant material that the grab would not close properly. Usually 0.1 m² of the bottom sediments was sampled, at particular sampling points.

A ring type insect net was used to collect flying imagines, especially Chironomidae, from selected stations along the Jukskei-Crocodile River system. In addition samples from various biotopes were brought back to the laboratory and larvae bred out. Some correlation was found between insects collected on the wing and those emerging in the laboratory.

(ii) Analysis of field samples:

Each sample was formalinized in the field by adding 2 or 3 cc of 40% formaldehyde. In the laboratory a sample was transferred to a metal sieve with 22 meshes to the inch. This sieve was placed in a conical net of the same mesh as used in collecting and the sample washed by a spray of water, which separated the sample into two portions: a "macro-sample" remaining on the sieve and a "micro-sample" washed through into the net. The macro-sample was then transferred to the counting chamber of the scanning stand, designed

at the request of the author by Mr. C. CILLIERS of the South African Council for Scientific and Industrial Research and shown in Plate 1, upon which Zeiss stereo optics were mounted. Large leaves and obscuring detritus were then picked out and the animals counted and identified to genera or wherever possible to species. This method was quicker and less tiresome than picking out the individual animals prior to counting. The micro-sample contained the smaller animals such as entomostraca, *Nais* spp. and juveniles of large nymphs and often large quantities of fine detritus. The bulk was usually so large that it was not practicable to sort and count all the animals, so a method of sub-sampling was devised which gave a relatively rapid assessment of the numbers present. This method of subsampling and its statistical evaluation is given in a separate publication (ALLANSON and KERRICH, in press). A brief description is given below:

The material of the micro-sample was transferred to an octagonal vessel and suspended, depending upon the volume of the sample, in either 100 cc or 200 cc of water. The contents of the vessel were then stirred mechanically, during which 25 cc was transferred by means of a wide-mouthed pipette to a square counting tray. The number of animals in the sub-sample were then counted and identified to genera or species under a conventional binocular dissecting microscope. Only one such count was required to obtain a binomial estimate of the number of animals composing the micro-sample.

2. THE PHYSICAL AND CHEMICAL CONDITION OF THE FLOWING WATER

Physical condition

Flow

During summer the main stream was fast flowing and subject to drastic flooding. The flow was irregular, and maximum daily flows varied from less than 30 cusecs to greater than 6,000 cusecs, as measured at the main weir between Stations 21 and 22 on the Crocodile River (Figure 3). The wet season tailed off into the dry season through the month of April and lowest flows were recorded during June, July and August, 1958 (Table 5). The dry season usually ended September or October with the onset of the summer rains.

In the Upper Reach it was not possible to measure the cusecs values of floods as the weir between Stations 5 and 6 only measured up to 26 cusecs. This means that the flow data for the Upper Reach in Table 5 for the summer months were for interflood periods only. The highest interflood flows were during September, October, January, February and March. November and December were

usually hot and dry and the flow in all reaches decreased strikingly; in December 1957, the flow fell to 7 cusecs, almost a dry season value.

The Modderfontein stream was the river's only important tributary in the transition between the Upper and Middle Reaches. During the wet season this stream contributed between 2 and 7 cusecs to the flow of the Jukskei River, depending upon the rainfall in its catchment and the manner in which effluent from the Modderfontein Dynamite Factory was released. However, peak flood waters in the Jukskei River held back the waters of this tributary and it was only when a peak had passed that they were released and flowed strongly into the main river. This was confirmed by a study of relative contributions using BEAUCHAMP's (1956) conductivity method. The percentage contribution of the Modderfontein stream to the flow of the Jukskei River is given in Figure 4. There was little correlation with rainfall, and the highest contribution (69 %) occurred when the flood peak in the main river had passed.

During flooding the Jukskei River was scoured out and little mineralized effluent entered the river. After flooding, the Modderfontein stream quickly restored the mineral content of the river (Table 4).

Above the confluence with this stream the Jukskei River showed during summer and winter a diurnal variation in flow which in the dry winter season was almost entirely due to sewage effluents discharged from Bruma and Sandringham Works. (Table 6).

While from the table of daytime observations it would appear that flow was highest during the morning, 24 hourly investigations showed that the flow reached a maximum at about 10 p.m. and fell away gradually to a late afternoon minimum. There were two explanations for this:

(i) The river above the Frankenwald weir was used extensively for land irrigation by market gardeners, so that a reduction in flow occurred during the day time, with an increase at night when irrigation ceased.

(ii) The peak flow from the Bruma and Sandringham Sewage Works, 9.5 miles upstream, which also caused a nocturnal increase in synthetic detergent foam and obvious deterioration in the quality of the river water.

In the Middle Reach the flow of the main stream was increased by the entry of the sewage streams which during winter received almost their entire flow from sewage effluents discharged from the Cydna and Delta Works. The Klein Jukskei River at Station 20a contributed very little to the flow of the main stream. Table 5 clearly indicates the increase in flow due to these tributaries, although the

Overall increase in flow during the wet season at Station 20a was also due to run-off and the flow from minor tributaries.

This is confirmed by a study of Table 7 which gives the flow in m³/sec of the major tributaries of the Jukskei River on particular days during winter and summer. The small increase between Stations 15 and 20a on the Jukskei River indicates very clearly how little run-off contributed to the flow at Station 20a during the winter season.

The considerably higher flow in the Lower Reach as measured at the main weir between Stations 21 and 22 was very largely due to the flows of the Crocodile and Hennops Rivers during dry seasons, but during summer this depended a great deal upon the extent of rainfall over the catchment. Although Table 5 does not reflect this feature, it was observed that during localized thunderstorms one or other stream, particularly the Jukskei River, caused a measurable flood at the main weir.

Temperature

River water temperature during summer varied in the flowing water between 17°C and 25.5°C. In quiet flats and pool sections, surface water temperatures rose to 29.5°C. In winter water temperatures in the Upper Reach varied between 8.0°C and 12.5°C during the day time. However, diurnal readings showed that the difference between dawn and 2 p.m. temperatures could be as much as 8°C. Furthermore, the air-water interface cooled so rapidly in winter that "syndet" foam, so characteristic of the Upper Reach, froze although the river water temperature remained well above freezing point. See Plate VI. This climatic effect was short-lived and it was only on very rare occasions that the slower moving flats and pools froze.

Middle Reach temperatures were slightly higher in winter than those of the Upper Reach, and those of the Lower Reach were markedly higher. (Table 8).

Turbidity

During summer and winter, turbidities were always high in the main stream and the Klein Jukskei River and were in part contributed to by the soils making up the catchment. But in winter, due to the reduced flow, the effect of sewage effluents upon turbidity was more marked. However, erosion of the river banks especially in the Jukskei and Klein Jukskei Rivers was continually taking place as these streams flow in relatively deep, denuded troughs.

The high summer mean (Table 9) at Station 5 in the Upper Reach of the main stream was due to a sand-washing plant on the banks of

the river which returned its wash waters to the river. The temporary nature of this turbidity was shown by the drop at Station 6, two miles downstream.

High turbidities in this system were not characteristic of polluted streams; the unpolluted Klein Jukskei River had high summer turbidities at Stations 19a and 20 (Table 9). During summer months, due to the practice of veld burning, the turbidity arose from exposed granite soils in the catchment area which contributed a clayey suspension not precipitated at the comparatively high pH of the river water.

2. Chemical condition

(i) Variations in mineral component (Table 9 and 9a)

pH: During summer and winter the mean pH and range remained fairly constant at about 7.6 and between 7.0 and 8.0. A slightly higher mean was found at Stations 21 and 22 in the Lower Reach because of the alkalinity of the dolomite over which the stream flows. Summer maxima in the Upper Reach resulted from sewage effluent outfalls or uncontrolled effluent discharges. For example, at Station 5 a summer maximum of 8.6 was recorded. This was due to wash water from sandwashing plants and the alkaline nature of the seepage from the compost installation on the river banks.

Dionic Conductivity: Sewage effluent outfalls from Bruma Sewage Works and the highly mineralized effluent coming in via the Modderfontein stream were the two most important agencies causing significant increases in dionic conductivity during the summer season. The effect of the Modderfontein stream was most serious as it was clearly noticeable throughout the remainder of the main stream. Dilution by tributaries with low conductivity reduced the conductivity of the main stream before the river entered Hartbeespoort Dam.

During winter the mean dionic conductivity at each station in all three reaches was higher than during the summer. This was as a result of the reduced flow in the system and was reflected by increases in total dissolved solid concentration. The higher minimum conductivity at Station 9a during winter was due to the irrigation of the farm lands at Leeuwkop Prison Farm. Notwithstanding the diluting flow of the Crocodile and the Hennops Rivers the mean conductivity during this season at Stations 21 and 22 was slightly higher than in summer.

Total Dissolved Solids: The variation in T.D.S. of the main stream was similar to that of the dionic conductivity. The reduction in river flow was the main cause of the winter increase in T.D.S., as there was

parallel reduction in sewage works outfall, and although the flow in the Modderfontein stream was reduced during this period (flow = 8 cusecs), on a proportional basis this stream was still contributing a T.D.S. load similar to that in summer. Dilution by the better quality waters of the Crocodile and Hennops Rivers tended to reduce the T.D.S. concentration in the Lower Reach.

Alkalinity, Calcium and Magnesium: The alkalinity of the river water was always caused by bicarbonate ions (pH 7—9). During summer the highest bicarbonate concentration means were found between Stations 2 and 6 in the Upper Reach. Downstream of this station there was a decrease in alkalinity during summer at Station 8 but the entry of the Sandfontein and Braamfontein streams immediately below this station increased the alkalinity so that at Station 10 it was slightly higher than at Station 8. During winter, as Table 4 shows, there was a noticeable increase in bicarbonate alkalinity throughout the waters of the main stream. This was paralleled by increases in calcium and magnesium concentration which at Station 10 showed increased means as well as minima. The reason for this was very largely the reduction in flow and the proportionately greater effect of the sewage effluent outfalls.

Total Hardness, Chloride and Sulphate: The river water was moderately hard. During winter and summer sewage works outfall and the inflow of the Modderfontein stream retained hardness at a fairly constant level in the Upper and Middle Reaches. Dilution by the softer waters of the Hennops and Crocodile Rivers caused, during summer, a reduction in hardness and chloride and sulphate concentrations at Station 21.

(ii) Variations in nutrient component, B.O.D. and O.A.

This component was made up of nitrogen-containing compounds of which ammoniacal nitrogen, nitrite nitrogen and nitrate nitrogen were the most important.

In Tables 10, 11, 12, 13 and 14 complete sets of data are given for the period November 1955 to August 1957. It was not possible to investigate the degree or rate of nitrification downstream of the entry, just above Station 2, of the Bruma Sewage Works effluent, mainly because of the many small weirs which impeded the flow of the river in the Upper Reach, but from the data available (Table 4) there appeared to be no evidence of an "oxygen-sag" in the Upper Reach downstream of the sewage works outfall. Oxygen was found to vary between 21% at Station 1 to 85% of saturation at Station 5. In February 1956, an oxygen concentration equal to 65% of saturation was noted in the river water at all but one sampling point.

If in the Upper Reach the chemical condition of the river above

Bruma Sewage Works outfall was taken as an arbitrary standard, the evidence indicated a clearly defined increase in concentration of nitrite N and nitrate N below this outfall. The increase in ammoniacal N was less consistent. These increases in concentration in the Upper Reach were not entirely due to the sewage effluent from Bruma, as sites of incidental pollution, e.g. at Station 5 near Alexandra Township were also responsible for often quite marked increases of ammoniacal N in May 1956 and March 1957, and nitrate N in June 1956 and August 1957. Comparison of the various nitrogen concentrations at Stations 2 and 6 showed, in general, a decrease in ammoniacal N concentrations and an increase in nitrate N concentration. This would support to some degree the view that mineralization below the point of sewage effluent entry might have been taking place. Any such process was completely masked in the Middle Reach by the serious nitrogen pollution delivered via the Modderfontein stream at Station 8. The tabulated data indicated that there followed a very marked decrease in concentration of all nitrogen compounds downstream of this point, mainly due to the diluting inflows of the Braamfontein and Sandfontein streams and the Klein Jukskei River between Station 8 and 20a and the Crocodile River between 20a and 21. Local conditions at particular sampling points tended to obscure this trend, e.g. incidental pollution at Station 9a and particularly Station 22, near Hartbeespoort Dam.

Evidence is available (see page 23) which indicates that some disproportionate decreases particularly of $\text{NH}_3(\text{N})$ and increases in $\text{NO}_3(\text{N})$ were due to nitrification.

Although the biochemical oxygen demand decreased in a general way downstream it varied considerably. The data presented in Table 13 indicated that the points of uncontrolled polluting discharge, e.g. at Stations 1, 5 and 9a were the most seriously affected. At Station 1 near the outskirts of Johannesburg maximum B.O.D. was always measured in the dry season. At Station 5 this demand was generally higher during the rainy season when seepage from the compost installation increased. Although this data indicated that from a B.O.D. point of view river quality had improved below the entry of the Bruma sewage effluent at Station 2, a study of the diurnal variations during summer and winter (p. 26) indicated that in this respect these data from snap-sampling procedures were misleading.

In Table 14 the 4-hour oxygen absorption values at stations in the main stream are presented. No very clearly defined trend was noticed in the Upper Reach, except that there was generally an increase in O.A. downstream of Station 1. However, as with B.O.D., local conditions altered this trend, e.g. at Station 5 in March 1957 when an O.A. of 23.60 p.p.m. was recorded. This was primarily

TABLE 10
AMMONIACAL NITROGEN CONCENTRATIONS IN PARTS PER MILLION AND TOTAL DECREASE
AND INCREASE IN EACH REACH OF THE MAIN STREAM

| UPPER REACH | | | | | | | | | MIDDLE REACH | | | | | | LOWER REACH | | | | |
|-------------|-------|------|------|-------|------|-----------|-----------|-------|--------------|-------|-------|-------|-----------|-----------|-------------|-------|------|-----------|-----------|
| 1 | 2 | 3 | 4 | 5 | 6 | De-crease | In-crease | | 8 | 9a | 9b | 20a | De-crease | In-crease | 21 | 22 | 23 | De-crease | In-crease |
| 1.91 | 4.70 | 4.80 | 2.20 | 0.34 | 0.90 | | 1.01 | | 4.20 | 0.95 | 0.00 | - | 4.20 | | 0.00 | 0.00 | - | | |
| 0.28 | 2.97 | 1.68 | 0.35 | 0.67 | - | | 0.39 | 157 | 29.40 | 5.26 | 6.20 | 151 | | | 1.00 | 0.00 | 0.80 | 5.40 | |
| 2.18 | 5.54 | 5.54 | 6.33 | 1.96 | 1.57 | 0.61 | | 60.20 | 35.60 | 51.50 | - | 8.70 | | | 6.20 | 48.70 | 0.00 | 15.90 | |
| 0.28 | 4.26 | 4.37 | 4.26 | 1.23 | 1.23 | | 0.95 | 6.66 | 8.84 | 1.10 | 29.50 | | 22.84 | | 2.00 | - | - | 27.50 | |
| 4.36 | 8.85 | 6.72 | 6.27 | 0.78 | 0.39 | 3.97 | | 18.50 | 42.00 | 10.20 | 7.20 | 11.30 | | | 0.11 | 0.00 | 0.00 | 7.20 | |
| 18.59 | 18.98 | 6.16 | 6.50 | 11.93 | 3.25 | 15.34 | | 53.60 | 48.80 | 4.10 | 8.90 | 44.70 | | | 3.50 | 0.00 | 0.00 | 8.90 | |
| 6.10 | 9.86 | 7.56 | 8.86 | 4.88 | 5.04 | 1.30 | | 7.00 | 36.70 | 12.20 | 13.40 | | 6.40 | | 1.70 | 3.30 | 0.62 | 12.78 | |
| 0.89 | 11.70 | 8.73 | 5.30 | 3.25 | 2.85 | | 1.97 | 60.00 | 11.10 | 4.70 | 17.20 | 42.80 | | | 0.50 | 1.50 | 0.17 | 17.03 | |
| 4.09 | 6.85 | 6.89 | 8.57 | 4.59 | 3.86 | 0.23 | | 80.50 | 79.00 | 32.20 | 13.50 | 67.00 | | | 1.10 | 0.10 | 0.00 | 13.50 | |
| 1.34 | 7.21 | 4.82 | 7.05 | 2.97 | 3.25 | | 1.91 | 70.00 | 103.50 | 51.10 | 36.10 | 33.90 | | | 0.00 | 0.70 | 3.80 | 32.30 | |
| 3.00 | 4.60 | 5.10 | 3.90 | 3.90 | 1.20 | 1.80 | | 49.00 | 35.20 | 17.60 | 18.70 | 30.30 | | | 0.00 | 0.00 | 0.00 | 18.70 | |
| 0.00 | 3.97 | 0.84 | 1.23 | 3.25 | 2.02 | | 2.02 | 189 | 79.70 | 59.40 | 22.30 | 166 | | | 3.00 | 11.30 | 9.40 | 12.90 | |
| 0.34 | 4.03 | 2.46 | 1.68 | 1.81 | 0.00 | 0.34 | | 50.40 | 48.30 | 34.60 | 27.10 | 23.30 | | | 0.50 | 0.40 | 0.10 | 27.00 | |
| 1.29 | 4.54 | 2.91 | 1.85 | 2.30 | 1.51 | | 0.22 | 32.90 | 10.40 | 16.50 | 2.00 | 30.90 | | | 1.20 | 0.20 | 0.00 | 2.00 | |
| 0.11 | 5.82 | 4.93 | 3.30 | 19.46 | 0.56 | | 0.45 | 40.60 | 9.70 | 9.18 | 6.10 | 34.50 | | | 3.00 | 0.50 | 0.00 | 6.10 | |
| 3.20 | 6.00 | 6.80 | 3.20 | 3.20 | 4.00 | | 0.80 | 12.18 | 6.90 | 2.07 | 0.40 | 11.78 | | | 1.70 | 0.10 | 0.50 | 0.10 | |
| 0.11 | 4.37 | 7.17 | 8.18 | 2.97 | 2.24 | | 2.13 | 41.70 | 39.80 | 18.90 | 8.90 | 32.80 | | | 1.30 | 2.20 | 0.00 | 8.90 | |
| 0.34 | 4.31 | 5.10 | 8.06 | 3.02 | 3.86 | | 3.52 | 43.30 | 46.40 | 27.50 | 8.62 | 34.68 | | | 1.10 | 2.00 | 0.70 | 7.92 | |
| 0.73 | 0.74 | 8.12 | 7.73 | 4.03 | 5.32 | | 4.59 | 43.10 | 43.90 | 17.60 | 8.62 | 34.48 | | | 0.17 | 0.22 | 0.00 | 8.62 | |

TABLE 11
NITRITE NITROGEN CONCENTRATIONS IN PARTS PER MILLION AND TOTAL DECREASE AND INCREASE
IN THE THREE REACHES OF THE MAIN STREAM

| UPPER REACH | | | | | | | | | MIDDLE REACH | | | | | | LOWER REACH | | | | |
|-------------|------|------|------|------|------|------|-----------|-----------|--------------|-------|------|------|-----------|-----------|-------------|------|------|-----------|-----------|
| ONS HS | 1 | 2 | 3 | 4 | 5 | 6 | De-crease | In-crease | 8 | 9a | 9b | 20a | De-crease | In-crease | 21 | 22 | 23 | De-crease | In-crease |
| 1955 | 0.23 | 0.38 | 0.45 | 0.40 | 0.30 | 0.33 | | 0.10 | 0.33 | 0.70 | 0.33 | 0.12 | 0.21 | | 0.03 | 0.03 | 0.03 | 0.09 | |
| 1956 | 0.15 | 0.28 | 0.45 | 0.38 | 0.65 | - | | 0.50 | 1.96 | 2.40 | 1.10 | 1.96 | | | 0.60 | 0.15 | 0.60 | 1.36 | |
| | 0.15 | 0.40 | 0.75 | 0.85 | 0.90 | 0.90 | | 0.75 | 0.95 | 1.50 | 0.56 | 0.23 | 0.72 | | 0.80 | 0.60 | 0.20 | 0.03 | |
| | 0.25 | 0.45 | 1.15 | 1.05 | 1.15 | 0.90 | | 0.65 | 0.60 | 1.40 | 0.05 | 2.00 | | 1.40 | 0.04 | | | 1.96 | |
| | 0.30 | 9.50 | 7.50 | 0.50 | 0.50 | 0.50 | | 0.20 | 0.40 | 4.00 | 0.28 | 0.26 | 0.16 | | 0.16 | 0.03 | 0.10 | 0.16 | |
| | 0.30 | 2.70 | 2.20 | 2.20 | 2.20 | 2.10 | | 1.80 | 1.40 | 1.04 | 0.48 | 0.28 | 1.12 | | 0.12 | 0.12 | 0.04 | 0.24 | |
| | 0.28 | 1.20 | 0.90 | 1.20 | 1.00 | 0.05 | | 0.23 | 0.08 | 0.13 | 0.03 | 0.60 | | 0.72 | 0.18 | 0.36 | 0.05 | 0.55 | |
| | 0.13 | 0.25 | 0.35 | 0.35 | 0.30 | 0.20 | | 0.07 | 0.45 | 1.40 | 0.25 | 0.01 | 0.44 | | 0.06 | 0.02 | 0.03 | | 0.02 |
| | 0.12 | 0.60 | 0.80 | 0.80 | 0.70 | 0.30 | | 0.18 | 0.90 | 2.10 | 0.90 | 0.46 | 0.44 | | 0.36 | 0.48 | 0.02 | 0.42 | |
| | 0.65 | 0.40 | 0.40 | 0.45 | 0.55 | 0.58 | 0.07 | | 1.10 | 2.50 | 1.60 | 1.30 | | 0.20 | 0.15 | 0.60 | 0.30 | | 0.15 |
| | 0.50 | 0.35 | 0.45 | 0.40 | 1.05 | 0.75 | | 0.25 | 1.90 | 12.00 | 5.00 | 0.80 | 1.10 | | 0.26 | 0.16 | 0.08 | 0.18 | |
| | 0.20 | 0.40 | 0.55 | 0.25 | 0.60 | 0.90 | | 0.70 | 2.00 | 11.00 | 8.00 | 3.80 | | 1.80 | 1.80 | 5.00 | 3.00 | | 1.20 |
| 1957 | 0.10 | 0.35 | 0.30 | 0.25 | 0.60 | 0.25 | | 0.15 | 0.40 | 1.30 | 1.20 | 0.88 | | 0.48 | 0.12 | 0.12 | 0.25 | | 0.13 |
| | 0.15 | 0.30 | 0.50 | 0.50 | 0.75 | 0.70 | | 0.55 | 0.85 | 3.00 | 2.40 | 0.25 | 0.60 | | 0.30 | 1.20 | 1.20 | | 0.90 |
| | 0.25 | 0.40 | 0.45 | 0.55 | 1.20 | 0.40 | | 0.15 | 0.60 | 1.90 | 0.30 | 0.56 | 0.04 | | 0.56 | 0.42 | 0.12 | 0.44 | |
| | 0.29 | 0.69 | 0.36 | 0.41 | 0.47 | 0.31 | | 0.02 | 0.30 | 1.36 | 0.73 | 0.20 | 0.10 | | 0.20 | 0.20 | 0.10 | 0.10 | |
| | 0.50 | 0.67 | 0.66 | 0.65 | 0.41 | 0.88 | | 0.38 | 1.90 | 0.99 | 1.19 | 0.40 | 1.50 | | 0.14 | 0.38 | 0.10 | 0.04 | |
| | 0.46 | 0.66 | 0.75 | 0.78 | 0.68 | 0.68 | | 0.22 | 0.88 | 1.48 | 1.03 | 0.40 | 0.44 | | 0.19 | 0.25 | 0.13 | 0.06 | |
| | 0.57 | 0.74 | 0.76 | 0.77 | 1.17 | 1.13 | | 0.56 | 1.29 | 1.97 | 1.33 | 0.80 | 0.49 | | 0.30 | 0.60 | 0.32 | | 0.02 |

(iv) The balance between $\text{NO}_3(\text{N})$ and $\text{NH}_3(\text{N})$ between Stations 9b and 22.

Table 16 shows the mass of dissolved nutrients or chemical demands expressed in grams/second relative to the average daily flow which pertained during the months of observation at two key sampling points in the main stream. The balances between ammoniacal N and nitrate N for the months of June and August 1957 may be interpreted as stoichiometric equivalents. Calculation has shown that in June 1957 a decrease of 15.48 grams/second of $\text{NH}_3(\text{N})$ was equivalent to a nitrate (NO_3) gain of 0.66 gm/cubic foot while the gain of 15.03 mgs/second for nitrate (N) was equivalent to an increase in concentration of nitrate (NO_3) of 0.71 gm/cubic foot. Similarly, for August of the same year the ammoniacal loss was equivalent to a nitrate (NO_3) gain of 0.70 gm/cubic foot while the nitrate (N) gain was equivalent to an increase of 0.77 gm/cubic foot. These estimates were made assuming that the respective increases in flow between Stations 9b and 22 were not responsible for any increases in either ammoniacal N or nitrate N so that the added flow acted as a diluent. The calculations made use of the degree of dilution to estimate what the concentrations of these substances, particularly of $\text{NH}_3(\text{N})$, would be if dilution were the only means of reducing the concentration of them.

From this data it was presumed that certainly during the months mentioned nitrification was taking place in the main stream. Where the balance was not struck the nitrate N increment was due to other factors which could not be monitored.

No equivalent data is given for the rainy season as the daily flow in the main stream and tributaries varied enormously and it was not possible to observe these changes in the same mass of water as it moved downstream.

This often disproportionate increase in nitrate N had considerable bearing upon the pollutionary state of the river. Where oxygen tensions were low the work of JEPSON & GREENE (cited by KLEIN 1957) indicated that the combined oxygen supplied by nitrates could be of great importance, since bacterial decomposition anaerobically is prevented by bacteria making use of this oxygen source. KLEIN also reported instances when nitrate salts, particularly of sodium, were deliberately added to rivers to assist in the removal of odours in standing and sluggishly moving water. Thus it may well be that the observed continual aerobic state of the main stream and its two main sewage polluted tributaries, the Sandfontein and Braamfontein was at least in part due to the maintenance of a high nitrate N concentration in the river, by both effluent discharges and natural processes of nitrification.

(v) Diurnal Variations in Dissolved Oxygen, 5 day Biochemical Oxygen Demand, pH and Temperature in the River System

This study on diurnal variations was carried out in the Upper reach at Frankenwald Experimental Farm between Stations 5 and 6 in the Lower Reach at Pelindaba (Station 22) and in the Blaauw-ink River at Zwartkoppies (Station 24). Dissolved oxygen samples were taken in each case from the end of a "Flat" by an apparatus similar to that designed by IRWIN (WELCH 1948). Water temperature and pH were measured at the same time.

At Frankenwald these studies were carried out once in winter (8th August, 1958) and once in the summer (13th February, 1958) when the river flooded six hours after commencement of sampling.

At Station 22 diurnal variations were studied on 20th and 21st March, 1958, and at Station 24 on the 5th and 6th December, 1957. Control data were obtained at Station 24 which is situated on a clean stream. At Station 22 the diurnal variation was studied where current velocity was less than 1 ft. per second.

The Stream at Frankenwald (between Stations 5 and 6).

The diurnal variations in dissolved oxygen, temperature, pH and O.D. are given for summer and winter in Figure 6. The main cause of these variations were the sewage inflows 9.5 miles upstream.

Minimal dissolved oxygen concentrations were found during the afternoon and not during the period just before dawn. During winter the minimal dissolved oxygen concentrations were low (3.32 p.m.) 33% of saturation and on the 18th August persisted for four hours. In summer the dissolved oxygen minima (4.22 p.p.m.) 45% of saturation under flooded conditions were slightly higher than in winter and only persisted for about one hour. The dissolved oxygen concentration rose during the night. In winter the rise was gradual requiring, on the 18th August, 1958, thirteen hours to reach concentrations similar to those found on the previous day. In summer, the data suggest that while the initial flood caused a significant decrease in dissolved oxygen concentration the rise during the night was more rapid than in winter.

pH variations followed a normal pattern in that the decreases were probably due to reduced or no photosynthesis in the diatom mats and on the river bottom. Water temperatures fell gradually in winter through the night to dawn, while in summer under flooded conditions water temperatures were reduced rapidly and thereafter tended to remain constant until the following day. Water temperatures were, however, never as low in winter as air temperatures which just above the river fell to -3.0°C .

Biochemical oxygen demands were higher during winter (15—5 p.p.m.) than during summer (11—5 p.p.m.). During winter this demand did not fall away from the observed maximum as rapidly as in summer. Furthermore, the observed maximum during the dry season occurred after the dissolved oxygen minimum, while during flooding the two values occurred at approximately the same time.

The Stream at Pelindaba – Station 22

In this deep slow flowing part of the main stream dissolved oxygen saturation did not fall below 60% at any time during twenty-four hours of 20th to 21st March, 1958. The dissolved oxygen concentrations remained at more or less 7 p.p.m. throughout the whole period (Figure 6). Water temperature remained constant at 23°C and pH varied little from pH = 8. The observed B.O.D. remained at about 2 p.p.m. except at 8.00 p.m. when a value of 4.31 p.p.m. was recorded.

Blaauwbank Stream – Station 24

The highest dissolved oxygen concentrations during December 5th, 1957, were found between 8.00 a.m. and 12.00 noon (Figure 6). Thereafter there was a slow but detectable fall in concentration to 9.00 p.m. The subsequent concentrations except that at dawn (5.00 a.m.) were not reliable because it became increasingly difficult to read the burette because of lighting faults. However, the data that was obtained suggested that there was no further significant decrease in oxygen concentration. Water temperatures varied between 19.0°C and 22.5°C; the highest temperature was measured at 2.00 p.m.

pH varied between 7.3 and 8.4, the highest value was measured at 4 p.m. These data showed that in clean shallow streams where there was little photosynthetic activity, such as the Blaauwbank River dissolved oxygen concentrations were highest in the morning and at their lowest during the night, although these minimal values never reached limiting concentrations. There was no evidence that concentration was lowest just before the dawn. In the polluted Upper Reach of the main stream this natural diurnal variation or "pulse" was completely overshadowed by snap flooding during the summer and a daily variation in water quality during the winter caused by the peak effluent discharge from Bruma Sewage Works earlier in the day. The effect of these two factors in the Upper Reach was to extend a normal dissolved oxygen "pulse" into a dissolved oxygen "sag" which especially during winter could last for a number of hours each day. The null hypothesis, H_0 that there was no difference between the oxygen variation in the unpolluted and polluted parts of this river system was rejected by the WILCOXON's matched pairs signed rank test, SIEGEL (1956) and Table 18.

I. GENERAL FEATURES OF THE PHYSICAL AND CHEMICAL CONDITION OF THE RIVER BOTTOM

Between the stony runs and granite cascades in the river system the pools and flats were mainly floored with quartzite sands. Mud only occurred in long stretches or where the rivers were dammed.

MORGANS' (1956) work in False Bay provided a useful method for the physical and chemical study of sediments, and with minor modifications the methods described by Morgans were used.

The river sediments were accurately classified on the basis of the Wentworth Scale and this gave a clear picture of changes during the wet summer season due to scouring by floods and the rapid deposition of the rolling load.

1. Physical condition

Dry Season

During winter there was usually no flooding and stream bottoms were stable. Figure 7 presents the phi cumulative curves of sediments in the streams comprising the river system.

From the median ϕ value it was possible to classify the bottoms on the Wentworth Scale as follows:

| ϕ | Median particle dia. in mm. | Classification | ϕ | Median particle dia. in mm. | Classification |
|----------|-----------------------------|-------------------|----------|-----------------------------|-----------------|
| -2 to -1 | 4 —2 | Granule | +2 to +3 | 0.25
0.125 | Fine sand |
| -1 to 0 | 2 —1 | Very coarse sand. | +3 to +4 | 0.125
0.0625 | Very fine sand. |
| 0 to +1 | 1—0.5 | Course sand | +4 to +8 | 0.0625 | Silt |
| +1 to +2 | 0.5—0.25 | Medium sand | +8 | 0.03 | Clay |

The following sediments occurred in the Jukskei-Crocodile River system:

- a) Main stream: Very coarse sand; coarse sand; medium sand; fine sand; and a silt and clay mix.
- b) Sewage streams: Granule; very coarse sand and fine sand.
- c) Klein Jukskei and Blaauwbank streams: Very coarse sand and medium sand.

The subsieve fraction (i.e. particles smaller than 64μ in diameter) was made up of humic particles, silt and clay. It was of considerable importance and its proportion was always calculated. Table 18 gives

the percentage of sediment which constitutes the subsieve fraction found during this period.

This table shows clearly that as the sediments become finer in texture the subsieve fraction increases. As sediments with high subsieve fractions were characteristic of deep quiet sections in the stream it was assumed that they were developed as a direct result of the decrease in current velocity caused in this system by artificial damming at intervals.

There were no clear-cut differences between the sediment types occurring in any of the three Reaches of the main stream. However, as Figure 7 and Table 18 suggest, in the Upper Reach, and the top of the Middle Reach, bottoms (Stations 3—8) were always sand, either coarse or medium. Deep and quiet water stretches were more characteristic of the Middle Reach and the sediments were finer. Station 23 in the Lower Reach is situated in the littoral of Hartbeespoort Dam near where the Crocodile enters the Dam and cannot, therefore, be considered as typically riverine.

Wet Season

Figure 7 shows very clearly that at all stations there was a shift in the median ϕ value in February, 1959.

As a result the sediments at Station 11 on the polluted Sandfontein stream were then classed according to the Wentworth Scale as "granule". However, at Station 13 on the Braamfontein stream the "granule" of the sediment was replaced by "very coarse sand". The sediments at Stations 12 on the Sandfontein stream and 21 on the Crocodile River were again classified as "very coarse sand" but as seen in Figure 7 the median ϕ value for Station 12 moved more into the middle of the range allowed in the Wentworth Scale. At Station 21 conditions changed little. At Station 6 the sediments retained their winter or dry season classification but as in Station 12 the median ϕ value shifted nearer to the lower limit of the range given in the Wentworth Scale. At Station 20 on the Klein Jukskei River the sediments were more clearly "medium sand" than during the dry season when as Figure 7 indicates the median ϕ values were arranged more closely around $\phi = +1$.

No clear picture emerged regarding changes in the subsieve percentage of sandy sediments during either the dry or wet seasons.

The relationship between current velocity and median ϕ value

Figure 8 (curve a) shows that there was a logarithmic relationship between current velocity and the particle size of sediments found on the bed of the main stream. HJULSTRÖM (SVERDRUP *et al.* 1942) has reported minimum average velocities at which particular particle

sizes are either eroded or transported. The minimum average velocity curve for transportation of various particle sizes is given in Figure 8 (curve b). Curve a was drawn up from dry weather flow velocities in the Jukskei River, and the median particle (size) diameter in mm of sediments existing at these velocities. Sediments that have settled require erosion before they can be transported. HJULSTRÖM's minimum average velocity curve for erosion is given in Figure 8 (curve c). The easiest particle to erode is, according to his data, about 0.5 mm and requires an eroding velocity of 20 cm/sec. This velocity increases rapidly for the largest particles reaching, e.g. a value of 100 cm/sec for particles of 10 mm in diameter. From the data available it appears that some part of the sediments at Stations 5, 21, 12 and 11 were eroded from the stream bed during the period of investigation. HJULSTRÖM (cited by SVERDRUP *et al.* 1942) makes it quite clear that curves b and c in Figure 8 relate to sediments of uniform texture. The unconditional acceptance of this data on sediments of variable texture such as those of the Jukskei River is, therefore, not very satisfactory. In this connexion an examination of the change in quartile skewness of particle size distribution confirmed that the character of the sediments did change.

As there is a linear relationship between the logarithm of skewness ($\log_{10} sk$) and the phi quartile skewness ($Sk_{q\phi}$), (KRUMBEIN & PETTIJOHN 1938) it was reasonable to express this moment of particle distribution in terms of phi (ϕ). MORGANS (1956) has used the following expression to estimate this transformation of skewness.

$$Sk_{q\phi} = \frac{(Q_{1\phi} + Q_{3\phi} - 2 [Md \phi])}{2}$$

and Table 19 gives the various estimates of $Sk_{q\phi}$. This data indicates that the majority of sandy sediment exhibited a negative phi quartile skewness, i.e. they were usually skewed in the direction of increasing coarseness of particle size. At Stations 3, 6, and 12 skewness increased from the dry season of 1958 to the wet season of 1959 (February).

This tends to confirm the view expressed above that erosion of the sediments did take place in the main stream which increased the coarseness of them, particularly during the wet season.

2. Chemical condition

Dry Season

Any chemical study of the river sediments must of necessity be superficial, in a survey of this type. Table 20 lists the results of conventional sediment analysis for each type of sediment that was found in the unpolluted and polluted streams. In this way it was hoped that

significant chemical differences would show up and that a correlation between fauna and chemical composition would be found.

What is immediately obvious from Table 20 is that as the percentage of the subsieve increased in the polluted area, there was a significant increase in carbon, calculated as C. This was particularly striking in the polluted rivers. To a lesser degree this applied to kjeldahl nitrogen calculated as nitrogen as well. Both sulphide and copper were significantly higher in concentration in the finer sediments than in the coarser ones. Ferric iron was not as closely correlated with the sediment types, and high concentrations were found in very coarse sand as well as in very fine or silt sediments. The only significant rise in pH was at Station 21 in the Lower Reach and was due to strata of Dolomite in the vicinity of this station.

In the Klein Jukskei and Blaauwbank streams which were unpolluted, the finer texture sediments were not found and comparison with the polluted main stream can only be made for very coarse, coarse and medium sands. If the chemical composition of the very coarse sands of the polluted streams at Stations 3, 11 and 12 is compared with that of an unpolluted tributary at Station 19, it is seen that carbon, nitrogen and ferric iron concentrations at this station lie within the range found in the polluted stretches of the river system. Sulphide sulphur was, however, higher than at Station 19. The carbon, nitrogen and ferric iron concentrations of the coarse sands at Station 20 on the Klein Jukskei stream did not lie within the concentration ranges for the same elements at Stations 3, 6 and 8: sulphide sulphur, however, was the exception. If the chemical composition of the medium sands is compared, the content of nitrogen, carbon and ferric iron in the unpolluted stream was generally higher.

There were some noticeable chemical differences in similar types of sediments from the upper polluted stations of the main stream and those lower down: cf. results from Stations 11 and 21 and from Stations 14 and 23 — Table 20.

Wet Season

If the data given in Table 20a are compared with that in Table 20 it is immediately obvious that total carbon (C) and kjeldahl nitrogen concentrations decreased markedly in February, 1959, in the polluted streams. Neither ferric iron nor sulphide (S) showed such clear-cut differences and for the purpose of this study were not immediately important. However, in the medium sands at Station 20 both carbon and nitrogen showed increases in February and these were not immediately explainable, except on the basis of bottom variability. This station was not subject to the scouring as were the polluted river stations and these increases may have reflected this feature.

The pH of the sediments were much the same as those during the dry season.

It follows from the data presented above that periods of serious sporadic flooding, which occurred during the wet season in the streams of the Highveld of the Transvaal, had two important effects on the sandy river sediment.

1. They changed the particle size distributions of the sediments usually to coarser types.
2. They reduced the total carbon and total nitrogen concentrations, the latter as measured by the kjeldahl method.

In the Sandfontein stream at Station 11 immediately below the outfall of sewage effluent and at Station 21 in the Lower Reach similar sediments were found but the carbon and nitrogen concentrations at Station 21 were much lower than at Station 11. Similarly, the fine fractions of Stations 14 and 23 were chemically very different and reductions in sulphide sulphur and copper were found at Station 23. In the first example (Stations 11 and 21) the data available were not detailed enough to explain these differences as a function of "self-purification", but merely indicated that where a sewage works discharged either activated sludge or humus tank floc with normal effluent, high carbon and nitrogen values in the sediments could be expected. The low sulphide sulphur concentrations in the sediments could be expected. The low sulphide sulphur concentrations in the sediments suggested that the interstitial waters of these sediments were freely well supplied with oxygen. In the second case, (Stations 14 and 23) the decreases in concentrations of the components previously mentioned might well have reflected increased oxygen concentrations in the sediments at Station 23. At Station 14 the surface water looked the same as the effluent of the central compartment of a conventional humus tank, and gas bubbles were constantly rising to the surface indicating that the bottom sediments were anaerobic.

The available figures show that in general there was no marked chemical difference between sediments common to the polluted and unpolluted streams of this river system. In streams where the marginal cover died down in winter this was to be expected as plant debris was continually falling into the stream and, therefore, other chemical criteria (if any) must be sought to separate polluted sediments from unpolluted ones.

I. A COMPARISON OF THE POLLUTION OF THE JUKSKEI RIVER WITH OTHER STREAMS.

The Jukskei River and its two main headwater tributaries received continuous flows of sewage works effluent almost at their source in

the hills of the Witwatersrand. During the rainy season these streams also received considerable volumes of storm water from the heavily populated areas of northern Johannesburg. In addition a continuous and highly concentrated inorganic nitrogenous effluent was received by the main stream from a nearby dynamite factory.

Since this study is the first detailed investigation of a supposedly heavily polluted stream it is as well to compare its main chemical features with those of other systems where pollution was considered to be less severe, and also to make comparisons with a severely polluted British river in a further attempt to assess the magnitude of the chemical pollution. In Table 21 observed ranges for accepted characteristics of water pollution are given both for the Jukskei River and for particular stations in a number of other rivers. What is immediately obvious from Table 21 is that the Upper Reaches of the Jukskei River were more heavily polluted by nitrogenous wastes (all of which had an organic origin) than any of the other streams for which data is quoted. From both HARRISON'S and KLEIN'S data it would appear that the authors' classifications were based largely upon B.O.D. and oxygen absorption; in the former case dissolved oxygen should be included. OLIFF'S complete data for the Bushman's River were not to hand so it may be that the values shown are too low. The range of dissolved oxygen and B.O.D. (see also Table 13) quoted for the dry weather flow for the Upper Reaches of the main stream fall well within the range provided by other workers' data. Thus it is possible to state that the pollution of the Jukskei River was chemically more severe than in other systems in South Africa, except perhaps in the Krom River, Western Cape if the nitrogenous component of the Jukskei River is not taken into account.

VIII. THE QUESTION OF "SIGNIFICANCE" OR "COMMONNESS" AS APPLIED TO SPECIES DRAWN IN SAMPLES FROM POPULATIONS FOUND IN RIVER HABITATS

ALLANSON & KERRICH (in press) have described a method suitable for the estimation of the numbers of animals in samples taken from habitats from polluted streams in the Transvaal. It was found that observed proportions of species in the sub-sample gave binomial estimates of the true proportions in the micro-sample. They did not specifically consider what happened when counts for the macro-sample were added in. As a result no estimate of true proportions present in the field sample was made. However, because the macro-sample count was only subject to observers error it was assumed that the macro- and micro-sample counts taken together gave a satisfac-

y estimate of the true proportions of species or numbers of individuals in the field sample.

However, while this method was of value in the numerical estimation of samples, it was not possible to decide what species or groups of closely related species found as a result of sampling could be used in the assessment either of the stream conditions or of the populations in which the samples were drawn. This led to an examination of the concept of "significance" (HARRISON & ELSWORTH 1958) as particularly applied to river ecology. In this present study the term "significance" has been changed to "commonness" as it is considered by the author that these terms are ecologically synonymous.

ANDREWARTHA & BIRCH (1954) pointed out that the commonness of a particular species may be looked at in two ways; firstly, with respect to some feature of the habitat such as nesting sites, or secondly, upon a numerical basis. So far all assessments of aquatic populations have been carried out using this latter basis, (PATRICK 1951, GAUFIN & TARZWELL 1952, BERG 1948, HARRISON & ELSWORTH 1958, OLIFF 1960), and until a great deal more is known about the ecology and life history of the species which make up these populations, freshwater ecologists must continue to rely upon purely numerical methods.

Where the sampling methods employed generate only qualitative samples, the relative incidence of species (usually expressed as %) has often been used in the description of plant and animal communities found in various river habitats. The same procedure was adopted during this investigation of a polluted river system.

HARRISON & ELSWORTH (1958) set a limit to this relative incidence, namely 5% below which a species was discarded. Species that were found with this incidence or higher for three months were considered "significant" and were used in the assessments of the populations in which the samples were drawn.

The setting of a lower level below which species were in the main discarded implied that such species were usually found in low numbers with a consequent low relative frequency. It was then necessary to discover whether or not there was any logical basis for this level other than an experienced observer's own assessment of which was important in any sample or sample series.

DEEDHAM & USINGER (1956) and GAUFIN, HARRIS & WALTER (1956) in America and BLISS & FISHER (1953) in England have attempted to describe the distribution of individuals of particular species in sample series by well-known mathematical expansions, of which the binomial is considered the most suitable.

It will be worthwhile at this point to consider the applicability of a distribution to HARRISON's data as well as to the data obtained

in this present study. The basic conceptions underlying the application of the binomial or its special case, the Poisson series to observed data are:

- (i) that the probability of a single event is constant in a number of trials (samples);
- (ii) that the samples are independent;
- (iii) that the number of trials is random.

Thus in the river surveys carried out to date, particularly in South Africa, while it may be reasonable to consider that the samples from any habitats were taken at random, the time lapse between successive samples was relatively large, e.g. one month, and it was not possible to consider such a sample series as consecutive. As a result the proportion p of any species (or its probability) has not been shown to be constant month by month (taking a number of months on a seasonal basis), as shown in the following table for *Pseudocloeon vinosum* taken from HARRISON's data sheets, for Station 5 (Wellington, Berg River) and *Austrocloeon virgiliae* taken from *Polygonum* spp. Station 23 (Hartbeespoort dam).

| Berg River
1951 | | | Hartbeespoort Dam
1956 | | | Berg River
1951 | | | Hartbeespoort D
1957 | | |
|--------------------|----------------------|-------|---------------------------|---------|--|--------------------|---------|-------|-------------------------|---------|--|
| March | 0/94 | p_1 | Nov. | 87/494 | | Aug. | 60/186 | p_6 | May | 160/271 | |
| April | 1/48 | p_2 | Jan. | 37/364 | | Sept. | 222/298 | p_7 | June | 48/3063 | |
| May | 0/131 | p_3 | Feb. | 107/581 | | Oct. | 123/203 | p_8 | July | 0/698 | |
| June | 45/146 | p_4 | Mar. | 14/724 | | Nov. | 13/48 | p_9 | Aug. | 30/4107 | |
| July | 185/324 ¹ | p_5 | April | 5/325 | | Dec. | 110/322 | | — | — | |

$$^1 \frac{m}{n} = \frac{185}{324}$$

If the proportions ($p_3 \dots p_8$) obtained from monthly winter collections had been found to be equal or very nearly so, then

$$\frac{m_3 + m_4 + m_5 + m_6 + m_7 + m_8}{n_3 + n_4 + n_5 + n_6 + n_7 + n_8}$$

is an estimate of

$$\frac{n_3 p_3 + n_4 p_4 + \dots n_8 p_8}{n_3 + n_4 \dots n_8}$$

which is a pooled estimate of p and has a useful meaning. If p for example, is 0.1 and if the three basic concepts underlying the application of the binomial distribution hold, then it would be possible to set approximate confidence limits for p , which would indicate whether or not a species should be discarded when describing the faunal association resulting from a series of samples from any habitat. Since

or the relative incidence will vary with the size of N (the total number of individuals found), it is of importance to note how the limits of a p also vary with changing N . When $N = 100$ these limits may be obtained approximately from HALD's Table XI whereas the following expression

$$\pm 2 \sqrt{\frac{m}{n} \left(1 - \frac{m}{n}\right) \frac{1}{n}}$$

gives a closer approximation for larger values of N .

In Figure 9 the effect of total sample size upon the 95% confidence limits of suggested minimum levels of relative incidence, e.g. 5% and 1%, is shown very clearly. The curves given in this figure are theoretical constructions. The values of N given on the abscissa represent the range of total sample size obtained by HARRISON using a net of 23 mesh to the inch, and by the use of a net of 58 mesh to the inch as in this investigation. For example, a series of five samples from the marginal vegetation at Station 5 in the Berg River gave on average, during the wet season, a total sample population of approximately 1,000 individuals, whereas the same number of samples from the marginal vegetation from the Jukskei-Crocodile River system produced on average 5,000 or more individuals. The table below compares the 95% confidence limits for 1% and 5% relative incidence for different values of N , so summarising the data contained in Figure 9.

$N = 1000$

5% ± 1.38 (36 — 64) individuals

1% ± 0.63 (6 — 16) individuals

$N = 5000$

5% ± 0.64 (218 — 282) individuals

1% ± 0.29 (35 — 65) individuals

This approach could only be used infrequently in the analysis of both HARRISON's data and the data obtained from this investigation. The month by month variation of p for the majority of species was found to be too large. As a result each sample was judged separately. If, however, the samples had been taken at random from the same environment each month, they could be considered to be nearly binomial. If so, then it was possible to place 95% limits for each relative incidence. Table 22 presents the analysis of samples taken from the marginal vegetation at Station 3 (Rietfontein) and from HARRISON's sampling point 5. The relative incidences together with their 95% limits are also given.

The data given in Table 22 and shown graphically in Figure 10 is mathematically in no way different from the previous data, but the data was drawn up from single estimates of the different proportions of species occurring in a population, and it is not a pooled estimate

as previously described. As seen particularly from Figure 10 the 95 % confidence limits set a limit on the lower level of relative incidence depending upon the total number n of individuals in a sample, e.g. where n is > 578 a 1 % relative incidence is reasonable. Where n is < 578 this lower level of incidence is no longer satisfactory and must be increased until the confidence limits indicate that in 19 cases out of 20 it will be reasonable to expect the appearance of any species. This means that a species which occurred below a particular level of relative incidence should be discarded purely on the grounds that in repeated sampling one could not be certain that individuals of the species would always appear and, therefore such species are of little value in deciding what really belongs to the habitat under investigation. There are obvious exceptions to this, but a knowledge of a particular species' biology will help the observer to place it correctly in the population composition, e.g. predators and species which show sudden and very short-lived blooms.

From this analysis HARRISON'S 5 % level of significance is more understandable. In the analysis of data presented in this paper a 1 % level of significance or commonness was chosen because the value of n per sample, due to the decrease in mesh size, had increased on average about 5 times over n found per sample in the Berg River. As a result a species or group of closely allied species was considered common if it showed a relative incidence of 1 % or more per sample, and to ensure that those species which bloom rapidly and die down equally rapidly were omitted, this incidence or higher had to be maintained for at least three consecutive months throughout either the dry or wet season.

In this way the objection raised in the first part of this study, i.e. the large variation in p is removed by the simple rule that pooled estimates of p may not be made. Changes in p above the lower level of relative incidence (or actual numbers where sampling methods were quantitative) were likely to follow particular aspects of a species' biology or seasonal preference, which are the subject of a separate section of this paper.

IX. THE RELATIVE ABUNDANCE OF SPECIES IN THE SAMPLES TAKEN FROM POPULATIONS OF THE MAIN RIVER HABITATS

Because of the comparatively steep profile of the main stream, current velocities were high and a linear oxygen sag did not develop, but was largely replaced by a diurnal sag, extending as has been shown previously (p 25) beyond that which was found under unpolluted conditions. As a result faunal associations similar to those now accepted as belonging to the polysaprobic zone of

KOLKWITZ and MARRSON (cf. HAWKES in KLEIN 1957) were not found in the river system. Biological responses to polluting substances were indicated by changes in the relative abundance of one or other species in a community.

FISHER, CORBET & WILLIAMS (1944) have suggested, for macrolepidoptera populations caught over a period of years, that the distribution of species among the individuals was best described by a logarithmic series, in which the greatest number of species was represented by single individuals and the least number of species by many individuals. However, WILLIAMS in a recent paper (1953) has shown for the same data that this is dependent on population size and that their data agreed more closely with PRESTON's model (WILLIAMS 1953 and PATRICK *et al.* 1954) namely that, when the number of individuals in a sample increases the distribution of the species tends to be more closely fitted by a log-normal curve. WILLIAMS using a $x \times 3$ geometric class interval instead of PRESTON's "octaves" has demonstrated that the data from the macrolepidoptera populations exhibited a truncated log-normal distribution with the peak class often occurring in either the second, third or fourth geometric class depending upon the population size.

The same relation between number of species (omitting the Chironomidae) and number of individuals was found to hold for pooled dry season data obtained from the marginal vegetation, stony runs and sandy sediments. The probit transformation of the cumulative species incidence as per cent was always found to give, as shown in Figure 11, a series of points through which a straight line could be fitted by eye, thus confirming the log-normality of the distribution.

The following table compares WILLIAMS' data with that from the Jukskei River.

| WILLIAMS' data for macrolepidoptera. | | | | Data from heterogeneous invertebrate populations, Jukskei River | | | |
|--------------------------------------|---------|----------------------------------|------------|---|---------|----------------------------------|------------|
| Individuals | Species | Ave. no. individuals per species | Peak Class | Individuals | Species | Ave. no. individuals per species | Peak Class |
| 43 | 37 | 1.16 | I | 3,246 | 51 | 63.64 | I |
| 233 | 120 | 1.94 | I | 2,034 | 54 | 37.7 | I |
| 1,900 | 300 | 6.34 | I | 3,004 | 44 | 68.3 | I |
| 2,173 | 306 | 6.95 | I & II | 12,951 | 49 | 244 | I |
| 9,900 | 461 | 21.47 | II | 21,669 | 41 | 528 | II |
| 19,900 | 531 | 37.48 | II | 90,360 | 54 | 1673 | I |
| 99,900 | 691 | 144.6 | III | 21,419 | 26 | 824 | I |
| | | | | 52,402 | 42 | 1248 | I |
| | | | | 33,472 | 32 | 1046 | II |
| | | | | 109,544 | 34 | 2434 | II |

It is obvious from this table that while the number of individuals from the Jukskei River samples was generally greater than the transitional population given by WILLIAMS (2,173 individuals), above which the peak class shifts to II, only three out of the ten populations examined showed a peak in class II, and the remainder had the peak in Class I. However, the number of species identified from the Jukskei River was considerably smaller than in a numerically equivalent population quoted by WILLIAMS for moths. The effect of this factor upon the absolute form of the population profile is not understood but this method of presentation has been useful for comparative purposes especially as regards those population characteristics which separate clean water from polluted water associations. This implies that such log-normal distributions effectively define the fundamental characteristics of species communities. PATRICK *et al.* (1954), studying the diatom communities in streams, found that equally satisfactory fits of their data could be made to negative binomical, truncated Poisson, or truncated log-normal distributions. But they maintained that since the truncated log-normal curve was more easily fitted to observed data than the other distributions... "it seemed the most logical one to use." They offer in support of this procedure the views of PRESTON and HUTCHINSON who have maintained that such a distribution represents the structure of many natural populations. WILLIAMS (1953) has summarised the implication of log-normality as follows:

- (i) log-normality implies a finite number of species although the number of individuals is theoretically unlimited;
- (ii) three parameters are necessary to define a log-normal distribution of which the third is its standard deviation and since this determines the rate at which the number of species falls off from the mode it becomes of value in describing a population;
- (iii) with increasing sample size a log-normal curve is sigmoid and flattens out as it approaches the limit of the total number of species in the populations being sampled.

The first of these indications makes good ecological sense. For even if considered alone it would support the view that log-normality is a more realistic model of the distribution of species in populations than is the earlier logarithmic series which implied an infinite number of species as well as individuals. The two other implications are followed up in more detail in subsequent sections.

1. The effect of pollution on the moments of the species individual distribution in the populations of each habitat

PATRICK *et al.* (1954) used the slide traps of a "Catherwood Diatometer" to obtain populations of diatoms from which the effect of pollution was observed. When it was required to increase the number of individuals involved in any analyses this was done by simply counting a greater area of slide. This type of approach was not possible in this study of the species distribution in the three main habitats of the Jukskei River and WILLIAMS' (1953) method of collecting over long periods was adopted in principle. Experience in rivers in the Highveld of South Africa has shown that during a clearly demarcated season, e.g. the dry winter, the number of and types of species composing the samples remained reasonably constant. Thus it was feasible to add up the number of individuals of each species which had been found by sampling over a period of two dry seasons. In this way numerically large populations were obtained. WILLIAMS obtained large populations of macrolepidoptera collected by light traps by increasing the period of trapping.

It is well known that pollution by organic wastes reduces the variety of species and increases the number of individuals of selected species. The application of log-normal theory to this fact pin points the magnitude of such changes in various habitats. In Figures 12a, b and c the species distribution in samples taken from unpolluted habitats in the Klein Jukskei River and the Blaauwbank River at Station 24 are compared with samples from polluted habitats in the main stream. It should be noted that the theoretical curves given in Fig. 13 were drawn from the median and the standard deviation estimated graphically from fractile diagrams obtained from the observed data. They do not represent the theoretical truncated log-normal curve, but indicate the shape of the curves which would occur if these distributions were complete and not truncated.

From the evidence available in Figure 13, the mode of the distribution from the polluted habitats fell between the mid-points of the third and fourth class interval, while that from the unpolluted habitats occurred between the mid-points of the second and third interval. Furthermore, the mode of the polluted distribution was approximately only one third of that found in the unpolluted streams. These data also suggest that the position of the mode was not dependent upon the number of individuals counted. PATRICK *et al.* (1954) found for diatom communities that the position was dependent on this factor. As a result this shift of mode must be regarded as a pollution effect coupled with the decrease in species number. The

increase in the height of the mode and its negative shift in the species distribution observed for example, in the marginal vegetation at Station 8 below the confluence of the Modderfontein stream over that at the upstream polluted Station 5 is indicative of a greater species variety at the former station. The numerical equivalence of the fauna at these two stations indicates that pollution was still affecting the community of this habitat at Station 8. The median and the standard deviation of these contributions are given below.

| POLLUTED | | | | | | UNPOLLUTED | | | | | |
|-------------------------|-----|-------------------------|-----|-------------------------|---------|-------------------------|-----|-------------------------|-----|-------------------------|---|
| Marginal
veg. | | Stony
Runs | | Bottoms
Sands | | Marginal
veg. | | Stony
Runs | | Bottoms
Sands | |
| log ₃ x s.d. | | log ₃ x s.d. | | log ₃ x s.d. | | log ₃ x s.d. | | log ₃ x s.d. | | log ₃ x s.d. | |
| Station 5 | 2.6 | 3.3 | | | | Station 19a | 1.4 | 2.3 | | | |
| Station 8 | 1.7 | 3.4 | | | | Station 19 | | 1.8 | 1.8 | | |
| Station 2 | | | 3.0 | 2.1 | | Station 23 | | | | 2.2 | 1 |
| Station 3 | | | | | 2.2 1.4 | | | | | | |

PATRICK *et al.* (1954) found similar changes within the diatom populations of polluted streams, which confirmed the conclusions they had drawn from many river surveys about the effects of pollution in American rivers.

2. The degree of truncation of a log-normal distribution and its relation to the complexity of the habitats

In Figure 14 the fitted cumulative distribution curves and the observed cumulative distribution polygons are given for three different habitats. If the point of truncation is considered to be at $\log_3 x = 0$, then an estimate of the degree of truncation may be obtained from the fitted cumulative percentage distribution. The following estimates of the degree of truncation were made:

| POLLUTED | | | | | UNPOLLUTED | | | | |
|----------|-------------------------|----------|--|-----------------|------------|------------------|-----------|--|-----------------|
| Stn. | Marginal
veg. | | | Bottom
Sands | Stn. | Marginal
veg. | | | Bottom
Sands |
| 5 | 23%(21419) ¹ | | | | 19a | 28%(3246) | | | |
| 8 | 26%(21669) | | | | 19 | | 17%(1482) | | |
| 2 | | 8%(1586) | | | 24 | | | | 7%(820) |
| 3 | | | | 4%(562) | | | | | |

¹) The numbers in brackets are equal to the total number of individuals counted.

WILLIAMS (1953) stressed the need for examining very large populations in order to confirm the eventual log-normality of species-individual distributions in natural populations. However, examination of the above data contradicts this opinion when applied to populations in river habitats. The degree of truncation of the distribution in the stony runs and bottom sandy sediments was observed to be considerably less than in the marginal vegetation. In both cases the number of individuals was smaller than in the marginal vegetation. The best agreement to complete log-normality was observed in the population from the sandy sediments at Station 24, on the unpolluted Blaauwbank River where the number of individuals observed was only 820 distributed between 16 species. This evidence supports the hypothesis that the efficiency of a sampling net of given mesh size is related to the complexity of the environment being sampled.

If the assumption that the total number of individuals is equivalent to the occupancy of the whole environment, and that the species represent niches (MACARTHUR vide HAIRSTON 1959), is reasonably valid, then it is possible to understand the meaning of the truncated and nearly complete distributions found as a result of sampling natural habitats.

Truncated distributions in complex habitats have two possible meanings:

(i) the sampler is picking up only those species existing in the habitat with critical dimensions greater than the diameter of the mesh opening or

(ii) due to the phenomenon of contagion (HAIRSTON 1959) the species do not occur in true proportion in the sample.

This latter point would tend to increase the number of species which were represented by only one or two individuals, since only a small part of a species "mosaic" would have been sampled. HAIRSTON points out. . . "that species that are less successful in competition are not only less abundant, but are able to maintain populations only in restricted parts of the environment to which they are well adapted." Thus, as pollution reduces the competition between species by removing the less tolerant forms, the degree of truncation of communities living under polluted conditions should be smaller than in clean water communities. The data given on page 40 confirms this point of view. At Station 5, one of the most affected sampling points in the main stream, the estimated degree of truncation was 82% of that at Station 19a on the unpolluted Klein Jukskei River. The reduction in the degree of truncation in the stony runs was more marked. At Station 2 in the polluted Upper Reach the estimated degree of truncation was 47% of that at the unpolluted Station 19.

Where a small degree of truncation is linked with a small total number of individuals, as in the sands at Station 24, on the Blaauwbank River and Station 3 in the polluted Upper Reach (Fig. 14) it must be assumed that the sampler is taking samples in which the proportion and types of species above a certain size limit is very similar to that actually existing in the habitat. Thus, this close approximation to log-normality in the sandy sediments of an unpolluted and polluted stream reflects the simple character of this habitat and the effectiveness of the sampling method.

X. THE IMPORTANT COMPONENTS OF THE FLORA OF THE MARGINAL VEGETATION.

The vegetation is composed of a variety of plant species which form this usually very productive substrate.

In the Upper and Middle Reaches of the main stream the grass *Pennisetum clandestinum* HOCHST. is very common and with *Polygonum lapathifolium* L. and *P. salicifolium* BRAUSS are the only important components. (Plate V). In the Lower Reach the *Polygonum* spp. remain important but *P. clandestinum* is replaced to a very large extent by other grasses such as *Echinochola stagnina* (RETZ) and sedges such as *Cyperus vegetus* WILLD. and *C. fastigatus* ROTTB.

In the Sandfontein and Braamfontein streams, especially in the polluted sections, the dominant species is *P. clandestinum*. At Station 16, in the unpolluted source of the Braamfontein stream, a greater variety of grasses and *Typha* sp. are common.

The unpolluted Klein Jukskei and Crocodile Rivers possess a very varied marginal vegetation flora including the common grasses, e.g. *Eragrostis atrovirus* NEES, *E. plana* and *Andropogon eucomus* NEES. The sedges are very well represented by *Cyperus vegetus* WILLD. and *C. largus* L. and *Scirpus corymbosus* ROTH. Reeds such as *Phragmites communis* L. are also common.

The erosion of the river banks in the Upper and Middle Reaches with increased urbanisation have resulted in the significant reduction in marginal flora. During winter there is considerable die-back of the marginal vegetation, especially in the Upper and Middle Reaches of the main stream and the banks are left bare with large quantities of rotting vegetation lying in the water. Hence any discussion of the biological findings must take into account this serious seasonal change.

XI. THE FAUNA: GENERAL OBSERVATIONS ON THE MAIN STREAM AND UNPOLLUTED TRIBUTARIES

Apart from the application of log-normal theory to the descriptive analysis of particular ecological concepts, as outlined in the previous sections, the arrangement of sampling data into geometric classes as shown in Figures 12 a, b and c and Tables 23a, b, 24 and 25 summarises a great deal of information. In the tables large changes in numbers of common species, or species which become common as a result of worsening or improvement in river conditions, are noted. OLIFF (1960) pointed out for his data that only large numerical changes could be considered significant with respect to changing environmental conditions. The same rule applies to the data of this study.

Only the fauna of the main habitats of the Jukskei-Crocodile River system during the winter of 1956 and 1957 is described in this section. During these periods the flow of the river was most stable, and the various effluents entering the system would exert their greatest influence upon the communities. For convenience of description the most abundant species belong to the "primary association" while the species which were less abundant, but whose presence could be relied upon in the samples, belong to the "secondary association".

1. The animal associations of similar habitats in the marginal vegetation of the polluted Upper Reach and the Klein Jukskei River

(i) **Pool-like stretches** (Stations 4 and 17).

Examination of Table 23a shows that during this investigation 20 species were found at both sampling points but often with different numerical representations. The remaining 15 from Station 4, near Alexandra Township were well known organic pollution indicators, e.g. *Tubifex* sp., *Limnodrilus* sp., *Platycyclops poppei*, *Glossiphonia disjuncta*, *Glossiphonia* sp. A and small numbers of *Psychoda alternata* and *Psychoda* sp. A.

Of the eleven species which were restricted to Station 17, the two pulmonate gastropods, *Anisus natalensis* and *Lymnaea columella* and the entomostracan *Chydorus globosus* were the most numerous, followed by *Ancylus* sp. A, *Anisops gracilis* sp. and *Lestes* sp. A.

This evidence suggested that the organic pollution of the Upper Reaches of the Jukskei River, coupled with the severe flooding especially during the wet season, limited the development of a

gastropod fauna in the pond-like stretches. However, while the first two components of the primary association, viz. *Nais* sp. and *Chaetogaster* sp. were found to be the same in both habitats, the third component had changed from *Chydorus globosus* to *Platycyclops poppei* at the main stream sampling point. The very numerous and varied Cladoceran fauna was a feature of this habitat in this river system.

(ii) **The trailing marginal vegetation** (Stations 3, 5 and 20).

Eleven species out of a total of 33 (excluding the Entomostraca with the exception of *Platycyclops poppei*) from the trailing margins at Station 20 were also found in the margins at Station 3, Table 23. Three of them, viz. *Rhabditis* sp., *Pseudagrion salisburyense* and *Platycyclops poppei* were present in far greater numbers at Station 3. The primary association at Station 20 was composed of *Nais* sp., *Baetis bellus* and *Chaetogaster* sp. There was, furthermore, a greater number of species represented by fewer individuals at this sampling point than at the polluted station, actually 18 to 11 after combining Class I and Class II.

In the trailing margins of Station 3 all the typical pollution indicators were present and all with the exception of *Psychoda alternata* in high numbers. The primary association was made up of *Baetis harrisoni*, *Nais* sp., *Chaetogaster* sp. and *Platycyclops poppei* followed by *Tubifex* sp. and *Limnodrilus* sp.

No other distinct habitats within the marginal vegetation were found. The pollution of the Upper Reach of the main stream did not produce drastic changes in the fauna of this habitat.

The Upper Reach certainly, between Stations 2 and 6, did show some evidence of self-purification and it would be of value to examine how the fauna of this habitat responded to this. The species composition of the trailing margins at Station 6 (Table 24) shows how obviously the associations had responded to the improved conditions. It is not necessary to repeat the species lists for Stations 3 and 5 and the reader is referred for comparison to Table 23b. The fauna of this habitat at Station 6 was defined by a secondary association of Rhabditids, *Pseudagrion salisburyense*, *Baetis harrisoni* and *Austroclleon africanum* followed by a primary of *Chaetogaster* sp., *Nais* sp. and *Platycyclops poppei*.

Below Station 6 the river received at Station 8 via the Modderfontein stream, the effluent from a chemical factory, which as previously described, constituted a focus of heavy mineral nitrogenous pollution. When the number of air-breathers and aquatic breathers was compared at these two stations as in the following 2 x 2 contingency table a significant increase in the number of air-breathers was found at Station 8.

The abundance of air-breathing aquatic species in the marginal vegetation above and below the confluence of the Modderfontein stream with the Jukskei River:

Dry Season 1956/57.

| | Above
confluence | Below
confluence | |
|--------------------------------|---------------------|---------------------|----|
| Number of
air-breathers | 5 | 14 | 19 |
| Number of
aquatic breathers | 34 | 27 | 61 |
| | 39 | 41 | |

$\chi^2 = 3.9$ with degrees of freedom = 1
At $P = 0.05$, the null hypothesis that there was no difference between the faunas is rejected.

This may confirm OLIFF's (1960) observation that mineral pollution increases the numbers of air-breathing species in the population. The secondary association at this station was made up of Rhabdocoels *Chironomus calipterus* and *Nais* sp., with a primary composed of Rhabditids and *Platycyclops poppei*. The preponderance of *Rhabditis* sp. was due to the large quantities of detritus formed during the winter by the dying back of *Polygonum lapathifolium*. The absence of *Baetis harrisoni* from the secondary association was due to the reduction in current speed through the trailing vegetation.

Since the river as it passed through its middle and lower reaches received no further serious pollution, an established recovery fauna was developed especially in the lower reaches. For example, (Table 24) in the trailing vegetation at Station 21, a primary faunal association composed of *Platycyclops poppei*, *Nais* sp. and *Chaetogaster* sp., and a secondary association of *Cheumatopsyche zuluensis*, *Centroptilum excisum*, *Baetis bellus* and *Baetis harrisoni* had developed.

2. The animal associations of the stony runs of the Main Stream and Klein Jukskei River

On the basis of the population profiles the fauna of this habitat indicated a greater sensitivity to pollution than did that of the marginal vegetation. An examination of Table 25 in which the species composition of each class is given for the important sampling points of the main stream and the Klein Jukskei River confirms this adequately. Comparison of the fauna of this habitat at Station 2 on the main stream and Stations 19 and 20 on the unpolluted Klein Jukskei

River during the dry season shows that there existed at the former station a primary association of *Tubifex* sp., *Chaetogaster* sp., *Nais* sp. and *Platycyclops poppei*; while at Station 19 a primary association of *Cheumatopsyche maculata*, *Austrocaenis* sp. A, *Baetis harrisoni*, *Simulium nigritaris*, *Nais* sp. and *Phaenocora foliacea*, and at Station 20 a primary association of *Euthraulus elegans*, *Phaenocora foliacea*, *Pseudocloeon maculosum* and *Baetis harrisoni* were found.

The reduction in number of species as a result of the pollution from Bruma Sewage Works was striking. In the stony runs at Station 19 and 20 between 24 and 35 species were found while at Station 2 only 18 were observed. Six species were common to Station 19 and Station 3, but the relative densities of each species at Stations 19 were reversed at Station 3. *Limnodrilus* sp., *Chaetogaster* sp. and *Glossiphonia disjuncta* were obviously more numerous under polluted than under clean conditions. However, this observation serves to underline that it is by no means unusual to find typical organic pollution indicators occurring with low frequency in samples from unpolluted rivers.

From Table 25, by noting the change in composition from class to class, particularly of the well known pollution indicators, and the addition of new species to the fauna, some indication was obtained of the response of these faunas to the self-purification of the main stream as it flowed through its three Reaches.

At Station 3, the incidence of *Tubifex* sp. and *Limnodrilus* sp. in the population was high, as at Station 2 three miles upstream, but there was a noticeable increase in total numbers over that at Station 2, caused by a dense population of *Baetis harrisoni* and an even denser population of *Pristina* sp. and *Nais* sp. This suggests that during the early stages of self-purification the high nutrient content of the water, coupled with nearly stable dissolved oxygen saturation, caused the development of large numbers of a few tolerant species (see page 48). At Station 6, while *Tubifex* sp. and *Limnodrilus* sp. were found in reduced numbers (Classes IV and III), there were no striking additions to the species populations except *Austrocaenis* sp. A, which occurred in Class III. Similarly, at Station 9b, the number of species had not increased over that of Stations 3 and 6, but some of the typical pollution indicators had been replaced by *Simulium nigritaris*, *Centroptilum excisum* and *Austroclaeon africanum*. At this station, while *Tubifex* sp. remained a member of Class IV, *Limnodrilus* sp. had increased in number and was found in Class VI. This change was in response to the slight increase in pollution from the agricultural activities in the immediate vicinity of the river. Furthermore, this sampling point was sited below the serious mineral nitrogenous discharge of the Modderfontein stream

and below the entry of the Sandfontein and Braamfontein streams which received sewage works effluent from Cydna and Delta Works. Such discharges would restrict the addition of sensitive species normally found in this habitat.

Table 25 indicates that no important changes occurred in this habitat below Station 3 until after the confluence with the Crocodile and Hennops Rivers. Station 21 is situated below the confluence of these streams. *Tubifex* sp. and *Limnodrilus* sp. occurred only in Class II, their place having been taken in the numerically higher classes by a variety of species, e.g. *Simulium nigritarsis*, *Cheumatopsyche zuluensis*, *Phaenocora foliacea*, *Cheumatopsyche maculata*, *Prostoma* sp. A and *Centroptilum excisum*.

Notwithstanding this important change in species distribution within the individuals collected, neither *Nais* sp. nor *Platycyclops poppei* had been displaced or had disappeared from the fauna. Their presence in high numbers indicated that even the Lower Reach was part of the recovery zone of the main stream.

At Station 22, seven miles below Station 21 and the last sampling point on the main stream before the Crocodile River entered Hartbeespoort Dam, a small reduction in numbers of species was noted (38 to 36). The evidence of nitrogenous pollution, mainly of an organic origin, was given by the shift in the position of *Limnodrilus* sp. and *Tubifex* sp., which species now occurred in Class VI. The presence of pollution was confirmed by chemical, diatom and bacteriological analysis (CHOLNOKY 1958 and KELLER 1960). It was later found that along one of the minor tributaries above this sampling point was a native location which possessed no satisfactory sanitary disposal methods and all wastes were deposited in the tributary.

3. The animal associations of the bottom sediments of the Main Stream, Klein Jukskei and Blaauwbank Rivers

The numerical density and composition of species in the sandy sediments will be found in Table 26. Counts for the sandy sediments of the Sandfontein and Braamfontein streams at Stations 11, 12 and 13 are included for comparative purposes, and little real difference is observed between these sediments and those at Stations 3 and 6.

Station 21 was the most recovered area of the main stream, and this was as evident in the bottom sands as in the other habitats. There was an extreme reduction in the species number in the sands at Station 8. *Limnodrilus* sp. was found in vast numbers and *Chironomus calipterus*, *Tanytus guttatipennis*, *Baetis harrisoni* and

Rhabditis sp. occurred but in very small numbers. This was adequate evidence of the toxic nature of the Modderfontein discharge, slightly above the sampling point, which decimated the partly recovered fauna as found at Station 6, although the conditions at Station 8 were suitable for large numbers of *Limnodrilus* sp. (20,000 individuals per 0.1 m²).

The species composition in sands in the unpolluted Klein Juk River at Station 19, and at Station 24 on the Blaauwbank River presented a somewhat different picture (Table 26). *Limnodrilus* was still important and was the dominant member of the primary association at Station 19.

The following table sets out the primary associations which represent the faunal conditions during the time of the survey at the key stations:

| Station | Primary association |
|---------|---|
| 3 | <i>Limnodrilus</i> sp. |
| 6 | <i>Tubifex</i> sp., <i>Limnodrilus</i> sp., <i>Pristina</i> sp. and <i>Chironomus calipterus</i> |
| 11 | <i>Limnodrilus</i> sp., <i>Platycyclops poppei</i> |
| 12 | <i>Limnodrilus</i> sp., <i>Ilyocyptus sordidus</i> |
| 13 | <i>Rhabditis</i> sp., <i>Tubifex</i> sp., <i>Limnodrilus</i> sp., <i>Branchiura</i> sp., <i>Dero</i> sp., <i>Chironomus calipterus</i> and <i>Platycyclops poppei</i> |
| 21 | <i>Nais</i> sp., <i>Austrocaenis</i> sp. A, <i>Platycyclops poppei</i> and <i>Tanytarsus nigricornis</i> |
| 19 | <i>Rhabditis</i> sp., <i>Limnodrilus</i> sp. and <i>Tanypus guttatipennis</i> |
| 24 | <i>Ilyocyptus sordidus</i> , <i>Tanytarsus nigricornis</i> and <i>Pisidium</i> sp. |

XII. THE FAUNA: NUMERICAL CHANGES IN COMMON SPECIES INCLUDING INDICATOR GROUPS.

Numerical changes in individual species down the main stream were described in a previous section. It remains, therefore, to describe the seasonal changes which took place in the fauna of each habitat and to describe what factor(s) played the most important role in affecting such changes. By examination of the fauna of a number of habitats by monthly samples, no conclusion can be drawn from density changes which were in all probability due to features of life history. For example, the mayflies undergo periods of emergence which may be unconnected to the actual frequency and timing of sampling. Thus, a paucity of individuals of particular species in a known habitat may not necessarily reflect serious environmental change, but merely that the sampling took place between the appearance of successive populations. In the absence of knowledge about the life history of our commoner fresh-water species, investigation must rely almost entirely upon repetitive sampling during one

two years, to ensure that associations of at least common species may be described.

1. Marginal vegetation and stony runs

(Tables 27a—d, 28a—d).

The most important single factor affecting the density of fauna in these two habitats was the serious flooding of the main stream during the rainy summer season (cf. OLIFF 1960 page 327). This tended to give particular species a false season of higher numerical incidence, but there were species which did exhibit valid increases in numbers during the dry season. Such species were *Nais* sp., *Chaetogaster* sp. *Pleuroxus aduncus*, *Platycyclops poppei*, *Chydorus sphaericus* and possibly *Baetis harrisoni*. Where these species were found in the stony runs their period of peak incidence was the same as in the marginal vegetation. Of those species typical of this habitat, *Cheumatopsyche zuluensis* occurred in greater numbers during the winter. The Platyhelminth *Phaenocora foliacea* appeared in its greatest numbers (495 per 1 sq. ft. Surber) towards the end of the dry season, 1956, and while absent during the following summer appeared again in the winter of 1957.

The most striking numerical changes due to flooding occurred within the Entomostraca. Planktonic species were always found in large numbers at sampling points where current speed was reduced or pool-like stretches developed. *Monia dubia*, *M. rectirostis* and *Simocephalus exspinosus*¹ were found in bloom proportions, particularly at Station 9a towards the end of summer.

The data for the remaining species was not of the right sort to assign to them any particular season of greater numerical incidence. The work of CHUTTER (in press) on *Pseudagrion salisburyense* has shown how dangerous it is to assign seasonal preferences to a species without a complete knowledge of its life history. For example, CHUTTER found that for this species of dragonfly there was a continuous exploitation of the habitat by all three stages in the life history. This, he maintained, was advantageous since the rapid flooding during the wet season and early and late frosts were factors which could have caused heavy mortality among either the eggs, nymphs or adults of this species. He pointed out that the catastrophes which cause simultaneous heavy mortality in all stages would be few.

¹The correct nomenclature for the species of the genus *Simocephalus* found in this river system has been given by HARDING (in press). Of the three species found viz. *S. exspinosus*, *S. vetulus* and *S. serrulatus*, only *S. serrulatus* appeared to be restricted to the cleaner waters of the Klein Jukskei River.

He found that the nymph population of *P. salisburyense* during the winter was divided into two size groups which he considered further reduced the likelihood of a catastrophic reduction of the whole population.

Other numerical changes

Notwithstanding the fact that the whole system so far examined belonged to HARRISON'S Zone IIIb, particular species became less abundant as the river flowed towards Hartbeespoort Dam. The numbers of *Cheumatopsyche thomasseti* and *C. afra* per sq. ft. are given in the following table for Stations 19 and 21. The drop in altitude between these two stations is 500 feet.

| | C. afra | | C. thomasseti | |
|-------|----------|----|---------------|-----|
| | Stations | | Stations | |
| | 19 | 21 | 19 | 21 |
| July | 11 | 0 | 0 | 21 |
| Aug. | 74 | 2 | 1 | 4 |
| Sept. | 43 | 1 | 4 | 6 |
| Oct. | 0 | 12 | 0 | 168 |
| Nov. | 4 | 0 | 5 | 4 |
| Jan. | 20 | 8 | 1 | 2 |
| Feb. | 0 | 0 | 2 | 4 |
| Mar. | 26 | 0 | 11 | 6 |
| April | 13 | 13 | 7 | 83 |
| May | 1 | 3 | 0 | 38 |
| June | 55 | 50 | 7 | 166 |
| July | 5 | 1 | 0 | 9 |
| Aug. | 6 | 0 | 3 | 5 |

This confirms HARRISON'S own observation on the same species that *Cheumatopsyche thomasseti* is more abundant in stony runs at low altitudes than *C. afra*, which in the Berg River occurred with maximum abundance in the foothills stony run zone. In this connection the temperature difference between Stations 19 and 20 was quite marked. The lowest water temperature recorded during 1956 at Station 19 was 8.8°C while at Station 21 it was 11.0°C.

This was not sufficient support for a further zonation of the main stream, as species which HARRISON had found to be characteristic of Zone IIIb of the Berg River remained as important members of the fauna of the main stream down to Hartbeespoort Dam.

2. Bottom sediments (Table 29).

The most continuous record of numerical change was made at Station 21. The paucity of fauna during February 1958 was due to

serious flooding. During the dry season there occurred quite rapid increases in numbers of individuals until in September (Table 29) a varied fauna was established. *Nais* sp. and *Pristina* sp. were preferentially winter forms. A similar trend was observed in the sediments at Station 19, while at Station 20 the damming of the river had caused pondlike conditions to develop, so that the effect of flooding upon the bottom fauna was not observed. No clearly defined seasonal preference for groups within the Chironomidae was found and the gaps in Table 29 were probably due to sampling procedure.

The effect of quartile skewness on the density of bottom sediment faunas

The information given in Section VI: 1 poses the question: Did the main constituents of the fauna and the total number of animals collected in a given area of river bottom reflect the change in phi quartile skewness? This data is supplied for the head streams of the system in Table 30. No clear-cut trend emerged and as the information indicates it was just as likely that small total counts would be associated with increased and decreased negative phi quartile skewness as with positive phi quartile skewness. This holds equally well for the numerical density of the common species or groups of species found in these sediments.

IV. THE FAUNA: THE CHIRONOMIDAE OF THE RIVER SYSTEM AND HARTBEESPOORT DAM

PAINE & GAUFIN (1956) and SCOTT (1958) have stressed the importance of a study of aquatic diptera, particularly Chironomidae, in relation to the hydrobiology of inland waters. PAINE & GAUFIN used the presence of particular diptera as an indication of pollution in Lytle Creek, Ohio, U.S.A.; and SCOTT carried out a most detailed investigation of the Chironomidae of the Great Berg River, in which the occurrence of netted adults was correlated with the species emerging from breeding-out aquaria. This was done because of a lack of knowledge of what species occurred in the Western Cape and also the difficulty of assigning specific status to larval or even pupal forms.

The same problems arose in the Jukskei-Crocodile River system, and although the study of the Chironomidae was undertaken along lines similar to those described by SCOTT (1958), the work could not be carried out in such detail. Key stations were chosen, in each reach of the main stream and along the unpolluted tributaries, where imagine collections were made and from where living samples were taken to the laboratory.

Collections made during 1957 and 1958 of pinned adults, both male and female, were sent to Dr. P. FREEMAN of the British Museum who kindly identified the material and described a new species. In addition the classification used throughout this work is that arranged by FREEMAN (1955, 1956, 1957, 1958).

The following stations were chosen:

1. Polluted Main Stream

Upper Reach:

Station 6 at the Buccleugh Road Bridge.

Middle Reach:

Station 20a at the Krugersdorp Road Bridge below the confluence of the Klein Jukskei River.

Lower Reach:

Station 21 at the confluence of the Hennops River with the Crocodile River, near the Hume Pipe Sand-Pumping Station.
Station 22 at Pelindaba below the road bridge.

2. Polluted tributaries:

Braamfontein Stream Stations 13 and 14 below Delta Sewage Works.

3. Unpolluted Tributaries:

Klein Jukskei River:

Station 19, near the Veldskoen Drive-in Theatre.

Blaauwbank River:

Station 24, near Zwartkoppies Picnic Paradise and Sterkfontein Caves.

4. Hartbeespoort Dam:

Station 23 near Meerhof Hospital. Living samples were taken from three biotopes: marginal vegetation, stony runs and sand or muddy bottoms.

RESULTS:

1. Marginal fringe netting

The following table lists the number of species of each subfamily found at the sampling stations. The greater number of species collected downstream of the polluted sections and in the clean stream is obvious from this table. As far as possible collecting at each station has been alike and the increase in species cannot be said to be due to more intensive collecting at the down-stream stations, except at Station 24 where collecting was carried on after dark with the help of car headlights.

Number of species found in each sub-family during 1957—1958.

| Stations | Number of species | | | |
|----------|-------------------|----------------|----------------|--------------|
| | Tanypodinae | Corynoneurinae | Orthocladiinae | Chironominae |
| 6 | — | — | 3 | 5 |
| 20a | — | — | 1 | 2 |
| 21 | — | — | 1 | 3 |
| 22 | 1 | — | 3 | 8 |
| 23 | 2 | — | 3 | 10 |
| 24 | 2 | — | 6 | 13 |
| 19 | 1 | — | — | 5 |

The sub-family Chironominae may be further divided into two tribes (FREEMAN 1957, part III): Chironomini and Tanytarsini. The following genera have been found to represent these tribes in this river system.

The generic composition of two tribes in the Jukskei-Crocodile River system. The number of species found in each genus is shown by a suffixing number.

| Stations | Chironomini | Tanytarsini |
|----------|---|-----------------------|
| 6 | <i>Chironomus</i> (4) | — |
| 20a | <i>Chironomus</i> (1)
<i>Polypedilum</i> (1) | |
| 21 | <i>Chironomus</i> (1)
<i>Polypedilum</i> | — |
| 22 | <i>Chironomus</i> (4)
<i>Polypedilum</i> (3) | <i>Tanytarsus</i> (1) |
| 23 | <i>Chironomus</i> (6)
<i>Polypedilum</i> (1) | <i>Tanytarsus</i> (3) |
| 24 | <i>Chironomus</i> (4)
<i>Polypedilum</i> (6)
<i>Lauterborniella</i> (1) | <i>Tanytarsus</i> (3) |
| 19 | <i>Chironomus</i> (5) | |

From these data it appears that in the polluted Upper Reach *Polypedilum* species were not represented and neither were the Tanytarsini which were absent from the Middle Reach as well.

The apparent absence of species of these genera from Station 19 was in all probability due to insufficient collecting since larvae of Tanytarsini type were found in biological samples taken from the marginal vegetation and stony runs. The Orthocladiinae were represented at Station 6 in the Upper Reach by only two genera, viz. *Trichocladius* and *Cricotopus*, the latter being particularly common and almost solely represented by *C. albitibia* WALKER. At Station 24 this sub-family was represented by four genera, *Cardiocladius*, *Limnophyes*, *Trichocladius* and *Cricotopus*.

The absence of Corynoneurinae is noteworthy. SCOTT (1952) states that this sub-family is commonly found in the colder upper zones of the Berg River. Zones I, II and IIIa as found in the Berg River are missing from the Jukskei-Crocodile River system and therefore the representative fauna will be either absent from lower zones or only poorly represented. Corynoneurid larvae have been found rarely in the clean streams and never in the polluted streams.¹ A complete list of species found by netting in the marginal fringe is given in Table 31.

2. Data from breeding out from various biotopes

Marginal vegetation:

The following table lists the species obtained by breeding out from a number of stations.

| Species | Stations | | | | |
|------------------------------------|--------------|---------------|---------------|--------------|-------------------------|
| | 6
18.8.58 | 13
22.8.58 | 14
27.7.56 | 20a
.7.57 | 23
8.4.58
12.8.58 |
| <i>Dichrotendipes pilosimanus</i> | X | X | X | X | X |
| <i>Chironomus formosipennis</i> | X | | | | |
| <i>Chironomus peringueyanus</i> | | | | | X |
| <i>Stictochironomus puripennis</i> | | | X | | |
| <i>Cryptochironomus</i> sp. indet. | | | | | X |
| <i>Tanytarsus nigricornis</i> | | | | | X |
| <i>Polypedilum wittei</i> | | | | | X |
| <i>Polypedilum vittatum</i> | | | | X | X |
| <i>Cricotopus scottae</i> | | | | | X |
| <i>Tanytarsus</i> sp. indet. | | | | | X |

¹) HARRISON *et al.* (1960) found that *Coryneura* was very common in Olifantsvlei. The species found by them appeared to prefer clean, slow flowing streams with weed beds.

There was no doubt that the commonest species found in the marginal vegetation at the stations examined was *Dichrotendipes bilosimanus*. At Stations 6, 13, 14, and 20a this species emerged almost to the exclusion of all other species. At Station 23 in the marginal fringe of Hartbeespoort Dam it was not possible to assign dominance to any species from the data available. However, living samples taken on 10.6.58 from the *Genlisea* sp. mats in deeper offshore water were apparently solely composed of larvae of *Cricotopus scottae* FREEMAN.

Stony runs:

The table lists the species found as a result of breeding out from living samples taken from these stations.

| Stations | 6
19.9.56
15.4.57
14.1.57 | 21
18.8.58 | 24
1.10.58 |
|-------------------------------|------------------------------------|---------------|---------------|
| <i>Cricotopus albitibia</i> | X | X | |
| <i>Cricotopus scottae</i> | X | | X |
| <i>Tanytarsus nigricornis</i> | | | X |
| <i>Polypedilum natalense</i> | | X | |

At Station 6 *Cricotopus albitibia* WALKER was the commonest orthoclad present and *C. scottae* FREEMAN was rarely found. At Station 24, the Orthocladiinae were replaced almost entirely by *Tanytarsus nigricornis* GOET., *C. scottae* was again present. The habitats at these two stations were similar. Current speed at Station 6 on 18.9.58 was 3.43 m/sec. and at Station 24 on 1.10.58 was 3.01 m/sec. The altitude difference between the two stations was small, 200', and was not sufficient to account for the striking faunal difference which was found. The evidence available suggests that *T. nigricornis* is not tolerant of the polluted conditions experienced by *C. albitibia* at Station 6.

Sandy and muddy bottoms:

The subsequent table shows the species found in the sediments sampled.

| Stations | Polluted | | Unpolluted | |
|--------------------------------------|-----------------------|-----------------------|------------------------|------------------------|
| | 6
22.8.58
Sandy | 14
— 7.57
Muddy | 19
10.3.58
Sandy | 24
1.10.58
Sandy |
| <i>Tanypus guttatipennis</i> | | | X | X |
| <i>Cryptochironomus graminicolor</i> | | | | X |
| <i>Dichrotendipes pilosimanus</i> | X | X | X | |
| <i>Chironomus calipterus</i> | X | | X | |
| <i>C. formosipennis</i> | X | | | |
| <i>C. cafferarius</i> | | | X | |
| <i>C. leucochlorus</i> | | | X | |
| <i>Stictochironomus puripennis</i> | | X | | |

At Station 6 *Chironomus calipterus* was the commonest species, while in the muddy sediments at Station 14 *Dichrotendipes pilosimanus* and possibly *Stictochironomus puripennis* were the most important. These species were in general the most important found in the polluted sections of the river system. This was confirmed by an examination of the larval forms found in these sediments. In the clean sandy sediments of Stations 19 and 24 *Tanypus guttatipennis* was common and at Station 19 four Chironomini species were found, although from the breeding tanks it was difficult to decide which species was numerically more important than the others. In the sandy sediments at Station 24 a further species was found, namely *Cryptochironomus graminicolor*. The reader is referred to Tables 27, 28 and 29 for numerical details about the sub-families and tribes known to occur as larvae in the various habitats.

3. A comparison of the results of breeding out and of netting.

There was reasonable correlation between the types of species found by the two methods. Obviously a large number of species was missed by the breeding out method, but an assessment of the common species was obtained from these studies. In the following table particular data from the more comprehensive tables given in the Appendix are listed.

The density of individuals in the stony runs per 1 sq. ft. (929 sq. cm.)

| Species | 1956 | | | | | 1957 | | | | | | | | | |
|-----------------|----------|----|----------|---|---------|------|------|-----|-----|-----|-----|-----|----|----|---|
| | J | J | A | S | O | N | J | F | M | A | M | J | J | A | S |
| Chironominae | | | | | | | | | | 12 | | | | | |
| Orthoclaadiinae | | | | | | | 10 | 4 | 8 | 36 | 50 | 15 | 10 | | p |
| Tanypodinae | | | 8 | | 1 | 4 | 2 | | 1 | 40 | 5 | | p | | |
| Chironominae | 80 | | 98 | | | | 42 | 1 | 36 | 94 | 374 | 385 | 50 | 35 | |
| Tanytarsini | | | | | | | | 8 | | | 1 | | 4 | | |
| Chironominae | | | | | | 10 | | 2 | 10 | 100 | 200 | 1 | 4 | | |
| Orthoclaadiinae | 35 | 22 | 256 | | 201 | 1424 | 50 | 290 | 319 | 426 | 194 | 13 | | | |
| Station 24 | Mar. | | Dec. | | Dec. | | 1957 | | | | | | | | |
| | Stickles | | Stickles | | Gravels | | | | | | | | | | |
| Orthoclaadiinae | 58 | | 124 | | 32 | | | | | | | | | | |
| Tanypodinae | p | | 2 | | 65 | | | | | | | | | | |
| Chironominae | | | 13 | | | | | | | | | | | | |
| Tanytarsini | | | | | 112 | | | | | | | | | | |
| Chironominae | | | | | 1 | | | | | | | | | | |

The overall importance of the Orthoclaadiinae in the stony runs of the river system is clear. Seasonal maxima appear to be during the winter months as reported by SCOTT (1958) for the Berg River, though not in association with strong flow. However, the data for station 6 tends to refute this and suggests that the summer wet season was the period of maximum abundance. It is difficult to concile these data and more information is required before an exact period of seasonal importance may be stated. The data from the stony beds at Station 24 indicates that the Orthoclaadiinae were more numerous where current speeds were high, as in the stickles, than in the gravels. On the granite slopes at Station 6 *Cricotopus albitibia* was the only Chironomid. The gravels harboured the greatest density of Tanypodinae and Tanytarsini and the data from the sandy sediments suggests that these species prefer this type of hard bottom to the stony runs in the main part of the stream. SCOTT (1958) reports other habitats for species of these subfamilies, e.g. the orthoclad *C. albitibia* was bred out from sandy bottoms with vegetation; *Tanypus guttatipennis* from the muddy bottom of a dam above Tulbagh Barrage; while *Tanytarsus nigricornis* was not reported at all from any habitat either by netting or by breeding out. In this respect it is of interest to compare the netted and bred-out

faunas of the Berg River and Jukskei-Crocodile River System. The subsequent table presents only those species in the above system which were not reported by SCOTT in the Berg River.

| | |
|-----------------------------------|--------------------------------------|
| Tanypodinae | Chironominae cont. |
| <i>Tanytus lacustris</i> | <i>Chironomus transvaalensis</i> |
| <i>Pentaneura (ablabyia) sp.</i> | <i>Chironomus peringueyanus</i> |
| <i>Pentaneura meilloni</i> | <i>Cryptochironomus graminicolor</i> |
| <i>Procladius brevipetiolatus</i> | <i>Dichrotendipes chambiensis</i> |
| <i>Procladius apicalis</i> | <i>Polypedilum wittei</i> |
| | <i>Polypedilum vittatum</i> |
| Orthoclaadiinae | <i>Polypedilum abyssinae</i> |
| <i>Cardiocladius oliffi</i> | <i>Polypedilum deletum</i> |
| <i>Cardiocladius latistilus</i> | <i>Polypedilum dewulfi</i> |
| <i>Cardiocladius africanus</i> | <i>Polypedilum allansonii</i> |
| | <i>Polypedilum tridens</i> |
| Chironominae | <i>Tanytarsus pseudomancus</i> |
| <i>Chironomus cafferius</i> | <i>Tanytarsus nigricornis</i> |
| <i>Chironomus leucochlorus</i> | <i>Nilodorum ?brevibucca</i> |
| <i>Chironomus transvaalensis</i> | <i>Microtendipes taitae</i> |
| | <i>Lauterborniella pulchra</i> |

The total number of species collected by both methods in the Jukskei-Crocodile River system was 46, so that more than half of the Chironomidae found were not represented in the Berg River. This difference was obviously due to zoogeographical changes. An attempt to compare these data with those of OLIFF (1960) from the Tugela River met with even less success, as only thirteen of the species he records were found in the Jukskei-Crocodile River. This is surprising for from a consideration of the purely aquatic larvae or nymphs the Jukskei-Crocodile fauna was apparently more akin to that of the Tugela River than to that of the Berg River – see page 64.

The well-known pollution indicators in Europe, viz. *Chironomus plumosus* and *C. thummi* are replaced in these latitudes by *C. calipterus* and *C. formosipennis*.

XIV. THE FAUNA: A TOLERANCE ANALYSIS OF SPECIES IN EACH HABITAT.

It is well-known that rivers polluted by organic effluents, e.g. sewage, either raw or purified to some degree, may be divided into three distinct zones: 1) Polluted 2) Recovery and 3) Clean. Many attempts have been made to break up the first two zones into a variety of sub-zones on the basis of either chemistry or biology, but these simple divisions underly in every case many of the involved systems of zonation which have been erected by previous workers.

otably LIEBMANN (1951), but which are often supported by little concrete evidence.

As a result of the chemical studies in the main stream, the recovery one has been divided into two: an upper portion where the oxygen concentration varies widely diurnally and a lower portion where the oxygen concentration did not vary greatly. This was an easily observed character, the effects of which were more tangible upon particular species than possibly the variation in other chemical components of the river water which were not directly toxic. Furthermore, low dissolved oxygen tensions are often responsible for increased toxicity of compounds. Thus, the acceptance of the variation in dissolved oxygen as a standard of reference for separation of the fauna seems at present to be a logical one to adopt.

The fauna was then divided (Table 32) into five tolerance categories: 1) Pollution 2) Recovery with variable oxygen 3) Recovery with constant oxygen 4) Cleanwater and 5) Ubiquitous. Using these and the observed variations in chemical composition of the river an attempt has been made to correlate the pollutionary state of the water with the faunal associations found.

In this paper an attempt is made to clarify the nomenclature used in KOLKWITZ & MARSSON's "Saprobiensystem" (vide HAWKES in KLEIN 1957), which was the first attempt at a solution of this problem in European rivers and has subsequently been used extensively by other authors. It was therefore unnecessary to erect yet another system of pollution classification for South African rivers (cf. HARRISON 1958b pp 326—327) but important to define each class of the saprobic system by means of the detailed information collected during the investigation. For this purpose a method developed by DAY (1959) for the analysis of records from biological studies in Langebaan Lagoon has been used in analysing the communities described in previous sections. The analyses are given in Table 33. From this table the definition of saprobia has not been based upon a vague summation of the numbers of species which according to KOLKWITZ & MARSSON have a definite saprobic classification, but upon the relative proportion of each category in the whole assemblage of common species. Thus, the greater the relative proportion of pollution indicators, the better the whole fauna could be described as indicating a polysaprobic state. In this way the study and definition of pollution in biological terms falls more into line with present day community concepts, stressed particularly by RICHARDSON (1929) and GAUFIN & TARZWELL (1952).

Since the pollution of the main stream never reached such serious proportions that well-known pollution indicators were the only population of the various habitats, ubiquitous species were found.

The presence of *Nais* sp., for example, in both polluted and unpolluted portions of the river system, serves to underline HARRISON's observation "that any pollution indicator will not only be found in polluted waters but will also have a natural habitat somewhere". The Klein Jukskei was a slow moving stream, the water of which was mainly turbid with suspended clay. As a result the trailing margins were not washed clean of detritus and so became the natural habitat for *Nais* sp. In the faster flowing Crocodile River neither the trailing margins nor the stony runs harboured this species in any numbers.

In Section VII the concentrations of the sanitary component of the river were compared with other rivers in South Africa and Great Britain. Chemically the main stream appeared to be considerably more polluted than these other rivers, yet the faunal associations did not altogether support this view. Therefore, other factors must be taken into account when pollution is assessed.

HARRISON (1958b) has drawn attention to the most important single factor affecting such an assessment. He said... "under conditions of rapid or torrential flow, many typical polysaprobic organisms would be swept away, and physical aeration would be so vigorous that heavy organic pollution would not necessarily be accompanied by anaerobic conditions." It has been shown in a previous section that there was very likely a logarithmic relationship between ammonical N: nitrate N ratio and current speed, such that as the current speed increased, so this ratio decreased exponentially. In this connection KLEIN (1957) quotes the work of JEPSON & GREENE who found that the nitrate content of water is of little value as an oxygen source, provided the stream is well oxygenated. If, however, deoxygenation takes place, then the combined oxygen supplied by nitrates can be of great importance in preventing anaerobic conditions. The nitrate N concentration in the Upper Reach of the main stream was always high, due in part to the high current velocity and further to the standard sewage works practice in this country of producing, as far as possible, a well nitrated effluent. The faunal associations found reflected such conditions although the ammoniacal N, oxygen absorption and biochemical oxygen demand were often higher than in rivers where current speeds were less.

There was no evidence of the existence of a serious and extended linear oxygen sag to typical of slow moving rivers in Europe and the United Kingdom. There occurred especially in the Upper Reach of the main stream a diurnal sag. This would have the effect of selecting those species which could withstand large daily variations in dissolved oxygen but which would die out under circumstances of a permanent linear sag. It is well-known that the toxicity of substances such as NH_3 to organisms is increased by decreased tensions of dissolved

oxygen. The period of low oxygen tensions in the main stream may, therefore, have been long enough, particularly in winter, to allow the median time of survival (BLISS 1937) of particular species to become an additional selection factor. The development of this type of physiological study in the laboratories of the National Institute For Water Research and the Department of Nature Conservation should give this hypothesis greater support in the future.

XIV. DISCUSSION

HARRISON & ELSWORTH (1958) and OLIFF (1960) have, in their assessment of their findings, laid the foundations of faunal zonation in South African rivers, and have suggested reasons for such zonation. In addition they have greatly extended our knowledge of the geographical distribution of known species, and in doing so have discovered a great many new ones. They have also shown that little or nothing will be achieved in studies of this type, unless the student is prepared to carry out exhaustive and time-consuming field trips, and later numerical analysis of the samples taken. These preliminary requisites were incorporated in the initial planning of this special study.

It was possible to include simultaneous investigations on the bacteriology of the flowing waters and the benthic diatom flora.

The incorporation of these disciplines into the investigations allowed as complete a study as possible to be made of the effect of organic and mineral pollution upon the biology of a river.

1. A comparison of the clean and Recovery III fauna of the river with the fauna of the Berg and Tugela Rivers.

The Jukskei-Crocodile river system was defined as an extended hard bottom stony run zone of the lower foothill type (HARRISON's Zone IIIb). As a result its fauna was expected to show similarities to equivalent portions of either the Berg or Tugela Rivers.

In this respect it is interesting to note that OLIFF's (1960) "Foothill torrent zone" occurs in the Tugela river at an altitude of between 4000' and 5000' with an average gradient of 10' per mile. The "Foothill sand bed zone" lies between 3000' and 4000' with an average gradient of 1000' per mile. As the average gradient for the Jukskei-Crocodile River is 30' per mile, it was considered intermediate between these two zones. Although OLIFF has used different terms to describe the zonation of the Tugela River, the physical features of the zones are very similar to the Berg River. In the following table,

the common fauna (by previous definition) of these physically similar zones is given for the Berg, Tugela and Jukskei-Crocodile Rivers.

The species from each river which were found to be common in the hard bottom stony run zone or its equivalent.

| a | b | c |
|----------------------------------|----------------------------------|--|
| Berg R; Tugela R. | Tugela R; Jukskei-Crocodile R. | Berg R; Tugela R; Jukskei-Crocodile R. |
| <i>Simocephalus vetuloides</i> | <i>Branchiura</i> sp. | <i>Simocephalus vetuloides</i> . |
| <i>S. serrulatus</i> | <i>Limnodrilus</i> sp. | <i>S. serrulatus</i> |
| <i>Austrocloeon virgiliae</i> | <i>S. serrulatus</i> | <i>Baetis harrisoni</i> |
| <i>Pseudocloeon vinosum</i> | <i>S. vetuloides</i> | <i>B. bellus</i> |
| <i>Baetis harrisoni</i> | <i>Baetis harrisoni</i> | <i>C. excisum</i> |
| <i>B. bellus</i> | <i>B. bellus</i> | <i>Austrocaenis</i> sp. A |
| <i>Centroptilum excisum</i> | <i>Centroptilum exisum</i> | <i>Neurocaenis discolor</i> . |
| <i>C. pulchrum</i> | <i>Pseudocloeon maculosum</i> | <i>Afronurus harrisoni</i> |
| <i>Austrocaenis</i> sp. A | <i>Austrocaenis</i> sp. A | <i>Aeschna miniscula</i> |
| <i>Neurocaenis discolor</i> | <i>Neurocaenis discolor</i> | <i>Micronecta scutellaris</i> |
| <i>Afronurus harrisoni</i> | <i>Afronurus harrisoni</i> | <i>Cheumatopsyche afra</i> |
| <i>Aeschna miniscula</i> | <i>Euthraulus elegans</i> | (11) |
| <i>Nychia limpida</i> | <i>Neoperla spio</i> | |
| <i>Micronecta piccanin</i> | <i>Aeschna miniscula</i> | |
| <i>M. scutellaris</i> | <i>Pseudagrion salisburyense</i> | |
| <i>Cheumatopsyche thomasseti</i> | <i>Plea pullula</i> | |
| (16) | <i>Laccocoris limigenus</i> | |
| | <i>Sphaerodema nepoides</i> | |
| | <i>Micronecta scutellaris</i> | |
| | <i>Cheumatopsyche thomasseti</i> | |
| d | <i>C. afra</i> | |
| Berg R; Jukskei-Crocodile R. | <i>Hydroptila capensis</i> | |
| <i>Prostoma</i> sp. A | <i>Aulonogyrys abdominalis</i> | |
| <i>Nais</i> sp. A. | <i>Simulium medusaeforme</i> | |
| <i>Simocephalus vetuloides</i> | (24) | |
| <i>S. serrulatus</i> | | |
| <i>Baetis harrisoni</i> | | |
| <i>B. bellus</i> | | |
| <i>Centroptilum excisum</i> | | |
| <i>Austrocloeon virgiliae</i> | | |
| <i>Austrocaenis</i> sp. A | | |
| <i>Neurocaenis discolor</i> | | |
| <i>Afronurus harrisoni</i> | | |
| <i>Aeschna miniscula</i> | | |
| <i>Cheumatopsyche afra</i> | | |
| (13) | | |

The evidence presented in this table, omitting Chironomidae and the greater part of the Simuliidae, indicates that the remaining com-

non fauna of the Jukskei-Crocodile system has a greater affinity to the common fauna of the Tugela river than to that of the Berg River. Twenty-four species were found to occur commonly in both the Tugela and Jukskei-Crocodile Rivers, but only thirteen were found in the Berg and the Jukskei Rivers. Of these thirteen species, the data indicates that eleven were common in all three rivers, and as a result must compose a part of the ubiquitous element of the fresh water fauna in Southern Africa.

2. The polluted river.

(i) This represents the first detailed study of a polluted river in Southern Africa. Notwithstanding its elevated position on the Transvaal Highveld, the river system and its polluted and unpolluted tributaries have a faunal composition which is somewhat similar to that discovered by HARRISON (1958) in the coastal plain, Berg River. In addition, the generic composition of the recovery fauna was in many ways similar to that in rivers in the northern hemisphere, e.g. *Baetis rhodani*, *Cricotopus sylvestris*, *Chironomus plumosus* (HYNES 1958); *Glossiphonia* sp., *Simulium vittatum* and *Pelostoma* sp. (GAUFIN & TARZWELL 1952).

HARRISON (1958), OLIFF (1960) and HYNES (1958) have stressed the importance of the physical characteristics of rivers, such as flow and silt loading, both on zonation and selection of species which make up characteristic associations. These factors have not been adequately stressed or evaluated by many of the previous workers in this field, mainly because the studies have been reported on slow flowing streams, where organic pollution effects have been considered to be almost entirely due to the well-known effects of deoxygenation – the so called “oxygen sag”. This study has shown that where the profile gradient is relatively steep, and rain falls usually in a restricted season of the year, the oxygen sag does not manifest itself, but is replaced by a diurnal sag. Consequently the length of the initial stage of recovery is short compared with the length of the stream. These factors result in conditions which biologically indicate less severe pollution, although the primary pollution of the river was equivalent to or even worse than that reported in slowly flowing rivers. This work is in answer to HYNES’ (1958) observation that the biological effects of less severe pollution are less well documented.

(ii) Bacteriological and algological studies. The author was indeed most fortunate to have been able to invite the aid of two specialists, Drs. P. KELLER and B. J. CHOLNOKY, who worked in close conjunction with him, and as a result their investigations were carried out at the same time as the chemical and faunistic studies.

Thus each survey was increased in value by being correlated into the whole concept of the study. It will suffice to deal only briefly with the conclusions of these separate studies as they have now been published. (See CHOLNOKY 1958 and KELLER 1960).

CHOLNOKY found that *Nitzschia palea* was consistently the most important diatom species in the main stream. This species is, according to this author, indicative of nitrogenous compounds in solution coupled with aerobic conditions. But CHOLNOKY warns against the use of single species in the assessment of water quality, and in the analysis of his data describes associations revealed by the "THOMAS-SON" method of analysis. The associations of species (in order of relative abundance) that were consistently present in each reach of the main stream were found to be:

Upper Reach:

Nitzschia palea – *Gomphonema parvulum* – *Navicula semilinum* – *N. confervacea*.

Middle Reach

Nitzschia palea – *Navicular semilinum* – *Gomphonema parvulum* – with *Achnanthes minutissima* at lower stations.

Lower Reach

Nitzschia hungarica (more particularly at Station 22).

While the associations given above were considered to represent the general composition of the diatom flora in the river, the analyses of samples, taken at different periods and from different parts of the river habitat, indicated in the first place that:

(a) the environmental factors were not constant in the river, and varied in a general way between summer and winter, especially in the lower reach;

(b) the species composition of associations found in different parts of a river sampling point were markedly different, and could be related to the physical characteristics of those parts of the habitats in which they were found. For example, Table VI (CHOLNOKY 1958, page 214) indicates clearly how very different the important species were when samples were taken from fast flowing water and from nearby standing water.

The diatom associations were also affected by changes in surface geology in the catchment area. The dolomite band that runs between Stations 21 and 22 in the Lower Reach increased the calcium and magnesium content of the river water. Table XXV (CHOLNOKY 1958) indicates clearly how this change was met by the increased relative proportion (25.8%) of *Nitzschia hungarica*, which this author maintained was indicative of nitrogenous pollution linked with a rise in pH.

This evidence suggested that the diatoms should be incorporated

into any definition of Saprobia which might arise from the study as a whole. In his paper, CHOLNOKY used the KOLKWITZ & MARRSON system and purely on the basis of the diatom associations found has described the saprobic conditions of the rivers examined. However, before commenting further upon this author's findings, KELLER's (1960) contribution from a bacteriological view point must be examined.

In the discussion of his paper, KELLER (1960) puts forward evidence which shows that, during the dry season, the proportion of organisms of faecal origin in the river water was higher than during the rainy season. These organisms were divided into two groups, namely *Enterococci* and *Escherizia coli*. He showed further that bacteriological self-purification took place down the length of the main stream, but was more marked in the Upper reaches of the Jukskei River. KELLER noted that the power of self-purification in the Middle and Lower Reaches . . . "seems to be somewhat impaired, due to discharges of industrial effluents." At precisely those regions where pollution, "as expressed by the proportion of faecal to non-faecal organisms" (KELLER, 1960), reached a high degree, as at station 5, the faunistic, chemical and algological evidence supported his contention. Similarly, at Station 6 bacteriological self-purification was quite marked during the wet and dry seasons, and this improvement in river water quality was confirmed by faunistic, chemical and diatom observations.

Such unanimous agreement could not be expected in all cases where comparative data was available. For example, at Station 21 KELLER reports a notable increase in the proportion of bacteria of faecal origin during the dry season, while during the wet season this proportion had decreased considerably compared to that at upstream sampling points indicating little bacteriological pollution. The data set out in Table XXIV p. 235 of CHOLNOKY (1958) does not support this and reverses the period of minimum pollution at this station. In fact, CHOLNOKY describes dry season association "(Probe 2)" as "typisch oligosaprobic." Chemical data tended to support this view while the faunistic data, especially from the stony runs, ran a middle course and suggested a position between β -meso- and oligosaprobic. The equal value of bacteriological data in helping to describe the degree of pollution is, therefore accepted.

(iii) A comparison between the species-individual distribution and the Tolerance analysis as regards the description of the pollution in the Jukskei River.

The main stream of the river system was not polluted by a single effluent but by a number of effluents, widely different in chemical

composition. The way they were released into the river together with the comparatively fast flow of water effectively changed the classical picture of response within invertebrate faunas of different river habitats. It was largely because of this that two different approaches were used to analyse the data in an attempt to understand the effect of such discharges upon the fauna of the river.

(1) The arrangement of the faunal data into $x \times 3$ geometric classes (Section XI) served to underline the composition of the primary and secondary animal associations and allowed the species-individual distribution of similar habitats in the main polluted Reaches to be compared with those downstream. This information was further summarised by comparing the moments, e.g. the median and standard deviation of the distribution which invariably took a truncated log-normal form. This approach was very useful in summarising a good deal of information, but while the change in the moments of this distribution could be related to the overall intensity of pollution, it was realised that a study of the effect of a single polluting discharge upon the invertebrate faunas would be required before a completely satisfactory description of this method of analysis could be made. Unfortunately, no such simple case was found in the Jukskei-Crocodile River system and is rarely found anywhere in South Africa. Furthermore, the description of a fauna in terms of the mode, median and standard deviation tells nothing of its make-up and for this reason the second type of analysis was considered worth while.

(2) The separation of the fauna into five categories as described in Section XIV was largely based upon the ability of its different components to withstand variable dissolved oxygen concentrations. This type of analysis provided, on a proportional basis, the contribution each category made to the assemblage of animals sampled. This method, however, does not make use of all the data available as it is restricted to common species. If, however, commonness is related to the probability of occurrence of any species as explained in Section VIII, it would be unlikely that important species would be omitted and the calculated proportions of each category could be expected to closely approximate to the type of animal-association found under a given set of conditions.

In addition to the reason given above, this type of information could be more easily compared with the data of CHOLNOKY (1958) and KELLER (1960) than with that obtainable from log-normal analysis. It was therefore included in the assessment of the saprobic state of the river system as given in Table 34.

Both methods of analysis require intensive sampling before any description of the composition of the fauna of a habitat can be made. The arrangement of species found in any association in geometric

asses gives an unbiased estimate of what is or is not important in the community and the shift of typical pollution indicators, for example, *Tubifex* sp. *Limnodrilus* sp. and *Psychoda* spp. from one class to another can reflect the improvement or worsening in river conditions. But like the tolerance analysis, this approach is dependent upon physiological requirements of particular species, and until these are known for at least the species which compose the primary and secondary association, the evidence lead in either method must necessarily be circumstantial and therefore open to criticism. The need for research into physiological problems associated with the distribution of invertebrate faunas in streams as pointed out in Section XIV cannot therefore be too strongly stressed.

(iv) The definition of saprobic states.

An attempt is made here to make a synthesis of these contributions, including the chemical data on the flowing water, and in Table 34 new parameters are given for the saprobic system when applied to conditions resulting from organic pollution of comparatively swiftly flowing rivers.

KELLER (1960) does not attach the various divisions of the saprobic system to his data but points out that on total count alone he was not able to classify individual sampling stations. Neither in KOLKWITZ & LARSSON's nor in LIEBMAN's recent re-appraisal of their classifications (1951) were bacteria included, except in the form of total counts. The following table indicates what numerical values were attached to each class: -

| | |
|-------------------------|---------------------------|
| poly saprobic | 1,000,000 organisms/ml. |
| — β meso saprobic | 100,000 „ |
| oligo saprobic | 100 or less organisms/ml. |

That these parameters are virtually worthless has been shown by KELLER (1960 cf. Tables I, II and IV). In addition CHOLNOKY (1958) severely criticises the underlying premises upon which LIEBMAN used his "Gütekasse" modification of it, by remarking... "Seine (LIEBMAN) Definition der Güteklassen ist aber leider nicht frei von Fehlerquellen der Kolkwitzschen schätzenden Methode..." CHOLNOKY's data (1958) was not directly available for inclusion in Table 34 but a careful study of the text and tables given revealed that it was not unreasonable to erect from his data three categories to which the most important diatom species could be placed. The categories are -

1. Well oxygenated water
with minimum N

2. Reasonable oxygenation of river water but chemical conditions very variable.
3. Reasonable oxygenation but with high nitrogenous concentration.

By expressing the relative incidence of each category in the whole population found at any sampling point, this data falls in line with the methods of representation of the faunistic and bacteriological data.

In the faunistic studies the animal associations have been described by use of log-normal procedures which were useful in giving an unbiased view of the species composition. A further method of analysis due to DAY (1959) was useful in pin-pointing the pollutionary state of the common fauna of these associations.

This type of evidence has then revealed that the pollution of the main stream resulted in α - mesosaprobic conditions in the beginnings of the Upper Reach varying to β - mesosaprobic at Station 6, and that in the Lower Reach β - mesosaprobic varying to oligosaprobic conditions occurred during the period of investigation. Furthermore, the Klein Jukskei River must be described as oligosaprobic varying to β - mesosaprobic. Thus no point in the main stream nor in the Klein Jukskei River could be unconditionally described as oligosaprobic.

Of particular interest was the relationship between the *Nitzschia palea*: "Nitzschia zusammen" (CHOLNOKY, 1958) at the polluted Stations 4, 6 and 8 and the nitrogen content of the flowing water.

The following table presents this data and the chemical composition of the flowing water at the time of sampling.

| Stations | 6 | 4 | 8 |
|--------------------------|-------|-------|--------|
| NH ₃ (N) ppm. | 0.39 | 6.27 | 60.00 |
| NO ₂ (N) ppm. | 0.50 | 0.50 | 0.45 |
| NO ₃ (N) ppm. | 7.00 | 10.00 | 50.00 |
| Total N ppm. | 8.29 | 16.77 | 110.45 |
| <i>Nitzschia palea</i> | 80.7% | 82.3% | 49.9% |
| „Nitzschia zusammen” | 89.5% | 90.7% | 59.1% |

There is, from this table, an obvious discrepancy between CHOLNOKY's (1958) view, that *Nitzschia palea* is indicative of high nitrogen concentrations in the flowing water, and what has been observed at the various sampling points. Since, however, the origin of the high nitrogen loading at Station 8 was the effluent from a dynamite

ctory nearby, the majority of the nitrogen-containing salts in the
ukskei River, below the point of entry via the Modderfontein
ream had an inorganic origin, whereas the nitrogen of the main
ream above this point was of organic origin. CHOLNOKY (1960,
ivate communication) holds the view that the nature of the origin
F the soluble nitrogen in river water may well be important. Present
alytical methods do not distinguish between the origins of the
trogen content of water. But it is well known how complicated is the
ycle of events leading to the presence of nitrogen from the breakdown
F proteins. Since diatoms are active metabolic units, it is reasonable
• suppose that the associations developed, especially of nitrogen
• indicators, were in direct response, not to the presence of nitrogen as
etermined by analytical techniques, (i.e. inorganic N compounds)
ut to the availability of nitrogenous break-down products of organic
ecay. The addition then of large quantities of nitrate salts, e.g.
NaNO₃ and (NH₄)₂CO₃, via an effluent, need not be reflected by a
apid rise in the so-called nitrogen indicators. In fact such additions
ay be directly toxic. This problem certainly requires further
vestigation. In support of this view, it should be noted that down-
ream of this sampling point, the relative proportion of *Nitzschia*
alea in the samples (CHOLNOKY 1958) only rarely reach values
equal to those found in the Upper Reach although the nitrogen
concentration was often higher than that found in this Reach. Where
quivalent relative proportions of *N. palea* were found, e.g. at
station 22, this was considered as a direct result of organic
ollution. In this case, the organic pollution came from a native
ettlement, the wastes of which had access to the main stream above
e sampling point.

The techniques and objectives of stream surveys.

Since the publication of the "Saprobien system" by KOLKWITZ &
MARSSON in 1908 and 1909, a great many biologists have dipped
their nets into streams with often only a perfunctory examination
F the chemical characteristics of the flowing water, and have at-
tempted to show that one or other part of the stream may be classified
according to the saprobic system. From these very varied studies
emerged an assemblage of so-called "indicator species" among the
plant and animal species which inhabited the freshwater environ-
ment. Notwithstanding the simultaneous advances that were being
made in the study of community ecology during the first half of
this century, water biologists, especially in Europe, stuck rigidly
• to the philosophy of "indicator species". Among these species were

many microscopic forms which were difficult to identify, but this did not prevent a large number of the larger aquatic invertebrate species from being overlooked.

In 1929 RICHARDSON pointed out that to judge pollution conditions upon the presence or absence of a number of single species was unsatisfactory. He maintained that the cumulative evidence of species associations must be taken into account. GAUFIN & TARZWEL (1952) have confirmed the validity of this approach, certainly as far as the faunal complement of river habitats is concerned. CHOLNOKY (1958) has shown the value of an exactly similar approach during his investigation of the diatom populations of the polluted Jukskei-Crocodile River. As a result, the freshwater ecological studies in South Africa have been carried out on this basis, and only as a result of the synthesis reported in this paper have species been divided into categories, which refer mainly to organic pollution. They are: -

- (i) polluted,
- (ii) recovery with variable oxygen,
- (iii) recovery with consistent oxygen,
- (iv) clean,
- (v) ubiquitous.

HYNES (1958) has criticised this approach in the work of PATRICK (1951) and WURTZ (1955), but it is the author's conviction that if biological studies are carried out simultaneously with detailed chemical investigations, these obviously rough but useful categories may be laid down for the species endemic to a river system.

It must surely be accepted that one of the first responsibilities of a biologist when entering a river system for the first time is to locate the source of pollution, both organic and mineral, the important features of surface geology (making a note of those characteristics which his experience will dictate may exert an effect upon the chemistry of the river water), the accessibility of sampling sites, and choosing only those where the habitats are varied or which are close to the points of entry of polluting discharges. KELLER (1960) has pointed out how valuable this kind of knowledge is in the interpretation of bacteriological data from sewage polluted streams. In all the river investigations, either already published (HARRISON 1958b; HARRISON & ELSWORTH 1958; OLIFF 1960) or at present in progress, a preliminary survey, mainly of the biological features, was undertaken before the final research program was drawn up. This study often had the effect of pin-pointing the more important problems to be investigated and prevented the investigator from wandering aimlessly in a mass of confused and unrelated data.

As the final assessment of river conditions has to be made upon a number of discrete samples from populations which occur in the typical habitats of streams, it is important to examine some of the underlying problems of sampling.

Since it is now generally accepted that all judgements about the effects of pollution on stream biota must be made upon communities of species, it follows that the sampling methods used must be effective in generating samples which accurately reflect the true proportions of species occurring in the habitat sampled. At no time will it be possible to collect all the individuals of a population. Where quantitative samples are taken it may be possible to compare densities in comparable habitats downstream, for example, of a polluting discharge. As samples in aquatic biology are usually taken by nets, a further restriction is laid upon the relation of sample to population, namely, the dimensions of the sampler's mesh. Individuals of species with critical dimensions greater than that of the net used will be retained while those individuals whose dimensions are smaller will pass through. MACAN (1958) has drawn attention to this detail while OLIFF (1960) maintained that the mesh used (1 mm) in the Tugela River study gave only minimal numbers for the larger invertebrates collected. It has, therefore, become standard practice in South African hydrobiological research to use samplers with a net of 0.288 mm mesh opening. This mesh size retains Entomostraca and even the smaller Chironomidae, for example, Corynoneurinae.

The analysis given in section IX has shown that the species distribution in the total numbers of individuals collected by this mesh was log-normal, and that the degree of truncation was largely dependent upon the complexity of the habitat sampled. Where the number of micro-habitats was considered large, as in the marginal vegetation, the degree of truncation in samples taken from unpolluted streams was about 30%. In simpler habitats, for example, the sandy bottoms of a river, the degree of truncation was about 7%. From these data it was reasonable to assume that the proportion of species found by sampling was a fair estimate of that actually existing in the habitat.

The application of log-normal theory (first used by PRESCOTT for terrestrial populations and later modified by WILLIAMS 1953) in ecological work of this nature allows an objective estimate to be made of the species composition of the primary and secondary associations in the populations under investigation. In this way, the requirements of community ecology are complied with and even refined.

It is common practice, in the study of populations, to consider only the "common or dominant" elements, and to disregard those which, in the opinion of the worker, fall outside this category. It is

this very opinion which is open to question. It is rare to find the authors of ecological papers attempting to define what "common" means when applied to their data. In fact "common" defies any sensible definition ecologically unless, as ANDREWARTHA & BIRCH (1954) pointed out, it is related to some feature of a habitat, for example, nesting sites or leaves of a tree, etc. Since fresh water ecologists can rarely, if at all, relate the individuals of a species to some measurable parameter of the environment, it follows that a species must be considered "common" on a numerical basis only. This implies that replicate, independent samples must be taken from a population, in order to estimate whether a species is common or not from the number of times it occurs. In this way a species may be defined as "common", depending upon the probability of occurrence of at least one individual in a sampling series. Note that this approach does not give many information on how numerous individuals of a species might be. Thus the concept of "commonness" and of "numerical dominance" are distinct criteria by means of which the importance of a species in a population may be judged.

This digression was made in order to emphasize the need, in fresh-water biological research, of carefully planned sampling of river habitats. This must be followed by a complete, or very nearly complete, census of the types of species, and individuals which represent them. With this type of data, the application of statistical procedures is made worthwhile and significant changes may be assessed. While this would appear axiomatic, the literature is crammed with examples of lazy biological procedure, which have involved at the most an examination of a netted sample on the banks of a river from which species were noted as Abundant (A), Common (C), Fairly common (FC) and so on, and the sample then discarded. In addition, the biological condition of a river is often judged only upon a series of single sample estimates, taken downstream of a pollution source.

Another aspect which requires more careful study is the choice of sampling apparatus. Hand nets still remain the most important tool for the collection of samples, but these nets give only qualitative samples and while it may be possible to compare one sample with another it is not possible to estimate the density of animals, as neither volume nor area of substrate are known. MACAN (1958) has briefly reviewed the more important bottom samplers designed to sample the fauna of stony streams, and from such a collection it should be possible to choose a sampler most suited to the habitat. For example, ALBRECHT (in press) has shown that SCHRADER's method of sampling stony bottoms in the Kirnitzsh stream was more suited to the conditions of the stream than were either the SURBER or MACAN's shovel

sampler. The tabulated data given by this author indicate that the co-efficient of variation was generally smaller using SCHRADER's method than using either of the other procedures.

It follows, therefore, that if due cognizance of these points is made during the initial planning of a stream survey, and if these are then linked with simultaneous chemical, physical and biological studies, significant correlations may be expected, upon which future policy for the management of river systems may be based.

HYNES (1958) remarks that, while the effects of gross pollution are in any event fairly obvious, it is the more subtle cases of slight pollution for which biological investigation is particularly suitable. Although the term "slight pollution" requires some definition, this statement summarises nicely the underlying reasons for many of the investigations at present in progress in this country. Gross pollution of a river system is usually so obvious that the public are made immediately aware of its existence, and in some cases there is a genuine attempt to correct matters. Specialists, however, are aware of the varied types of subtle pollution which endanger one or other use to which a river system may be put, but which appear on superficial examination to be causing little or no change in either the physical, chemical or biological condition of these waters.

To a country like South Africa this type of pollution is the most important. Since a great many of the small head-water streams from the Witwatersrand watershed are eventually caught up in irrigation dams, the maintenance of the many small catchment areas in a state of comparative "cleanliness" is of some importance. During the past 25 years, the northern suburbs of Johannesburg have developed, and with the advent of modern sewerage and sewage works practice the head-waters of the Jukskei-Crocodile River system have received a steady 11 million gallons of purified sewage effluent per day. The result of this has been that Hartbeespoort Dam, 50 miles to the North, has during these years been converted from an oligotrophic state (HUTCHINSON, 1933) to an eutrophic state, with an extensive anaerobic hypolimnion during the hot wet summer. This single example of the effects of river pollution which never resulted in polysaprobic conditions serves as adequate support for a more reasoned approach in deciding the objectives of stream surveys. Thus modern objectives should be directed more to an elucidation of the effects of "subtle" pollution than to the description of the physical, chemical and biological condition of streams which receive "gross" pollution. After all such conditions are well documented and do not vary greatly from one river system to another.

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| | |
|---------------------|-----------------|
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| Dr. J. OMER-COOPER | Dystiscidae |
| Dr. K. M. F. SCOTT | Trichoptera |
| Dr. B. DE MEILLON | Simuliidae |
| Dr. P. BRINK | Gyrinidae |
| Mr. M. CHUTTER | Zygoptera |
| Prof. B. BALINSKY | Anura |
| Dr. K. H. BARNARD | Brachyura |
| Dr. E. MARCUS | Platyhelminthes |
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Figure 1: The Jukskei - Crocodile River system showing sampling Stations and land usage.

- 1 Residential area of Greater Johannesburg and other townships.
- 2 Grazing land.
- 3 Regions of intensive agriculture.

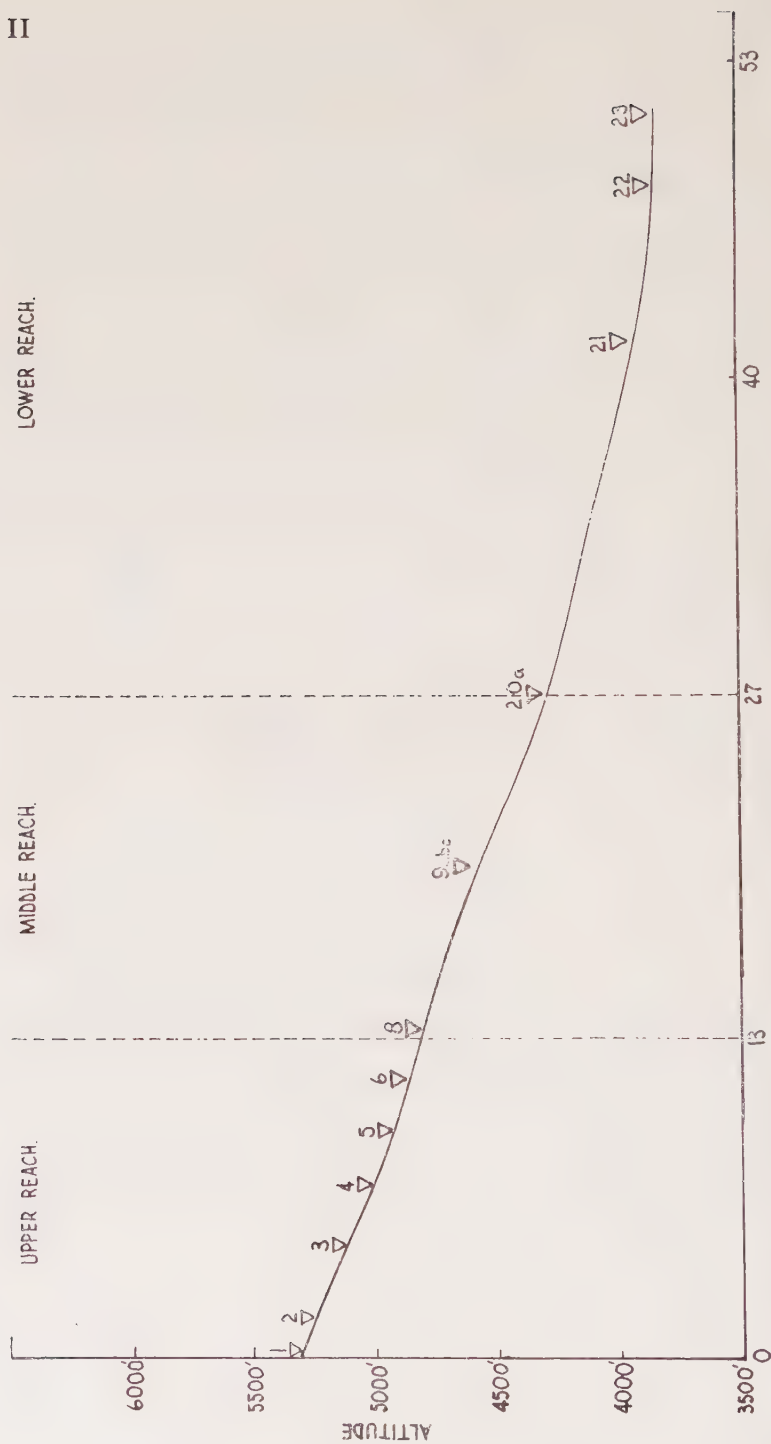


Figure 2: The profile of the Main Stream

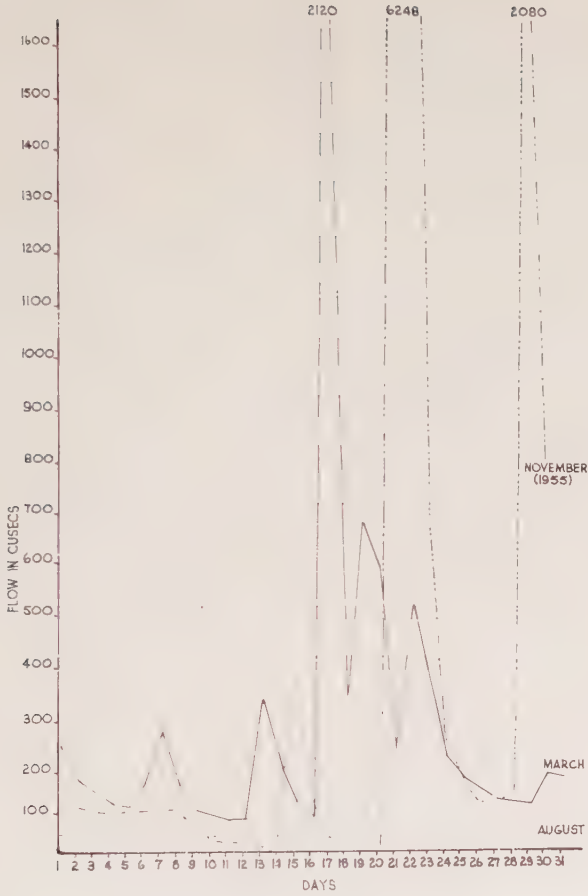


Figure 3: Variations in the flow of the river system as measured at the Kalkheuvel weir near Station 22.

IV

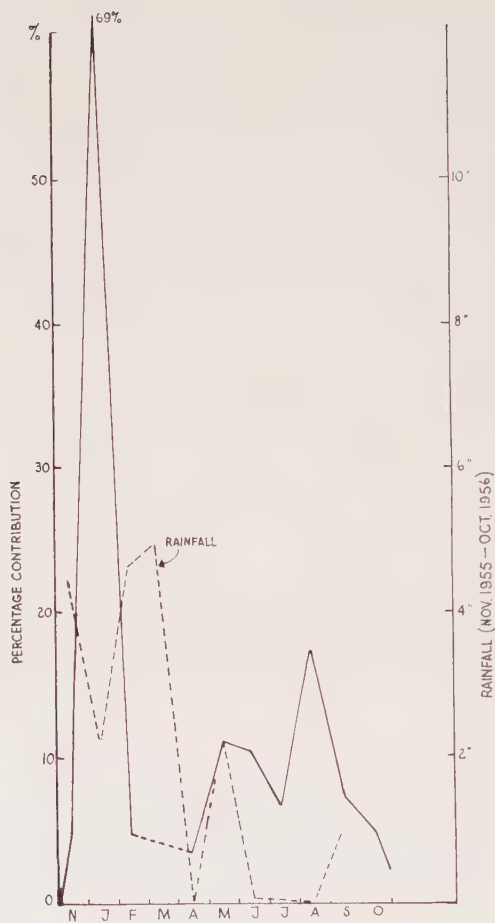


Figure 4: Percentage contribution of the Modderfontein stream based on Beauchamp's conductivity method.

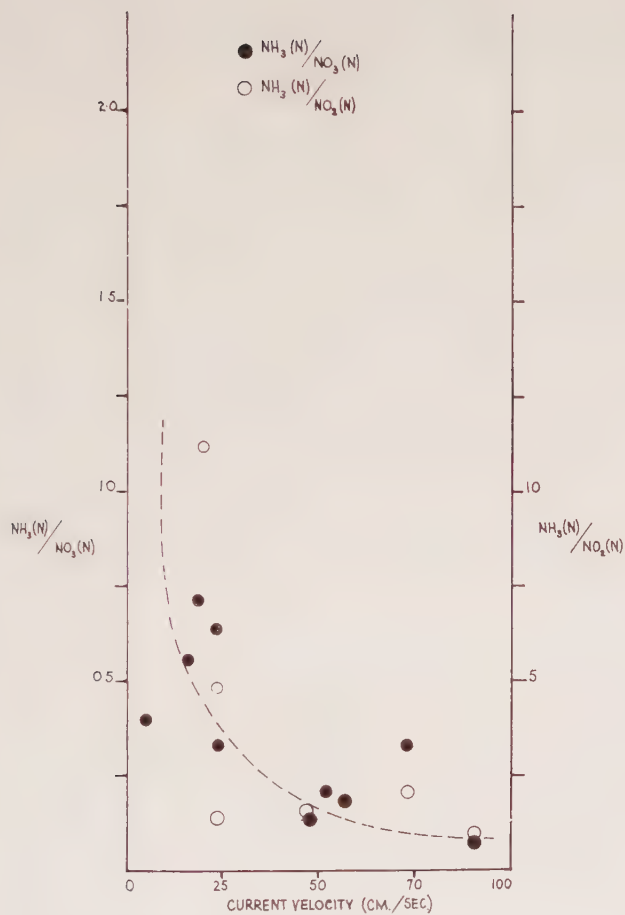
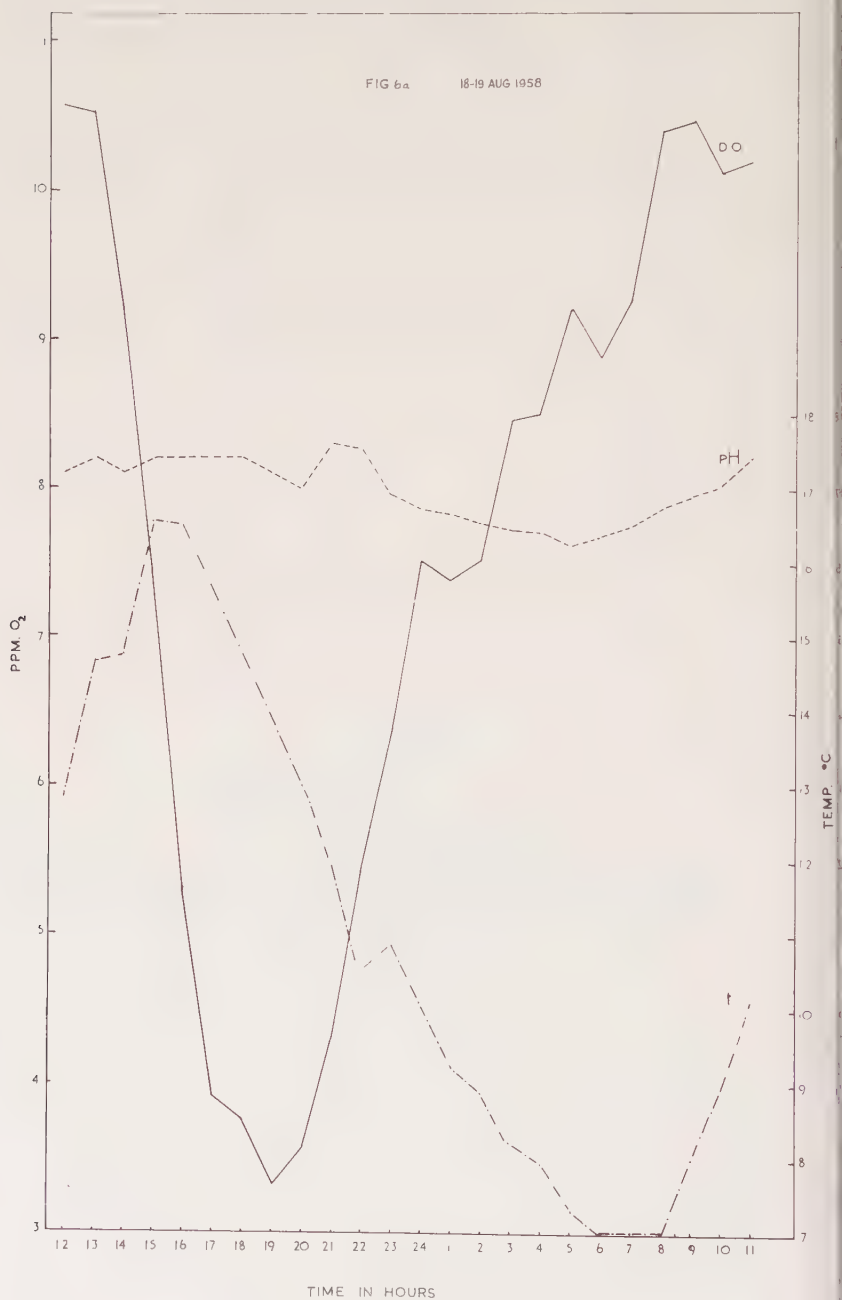
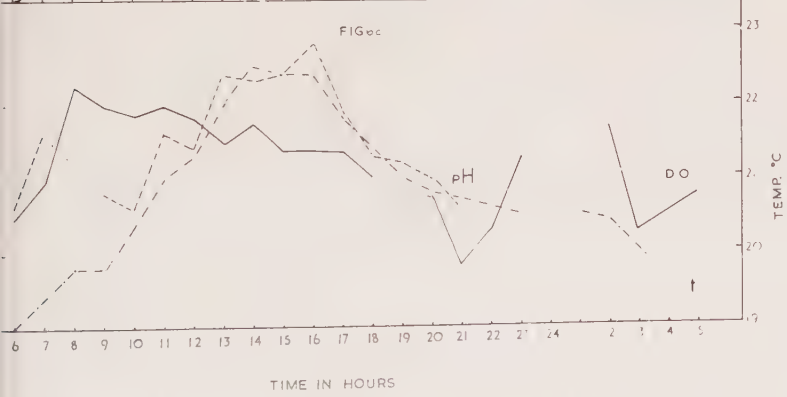
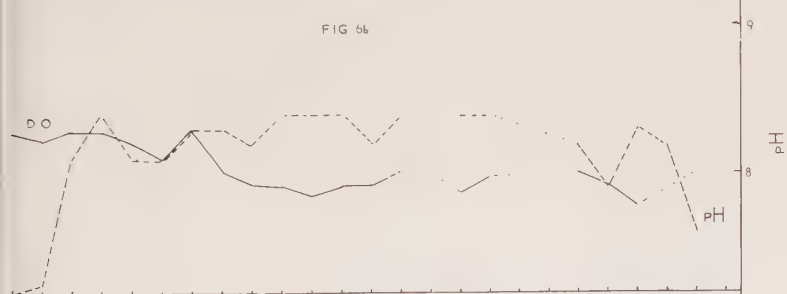
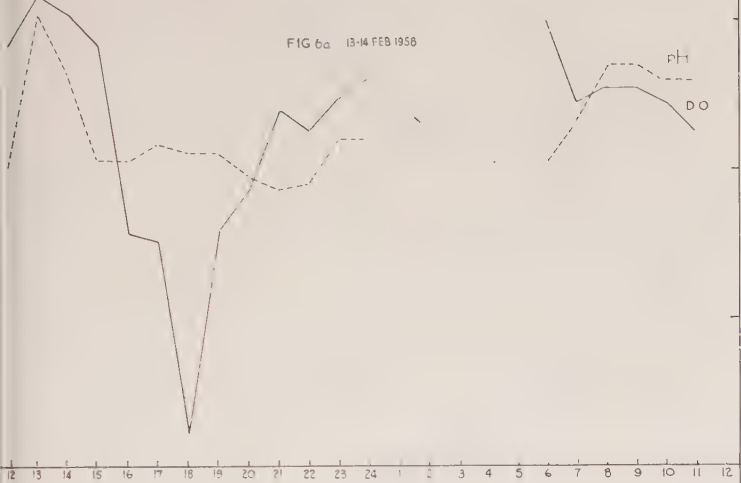


Figure 5: The relation between current velocity and the ratio of $\text{NH}_3(\text{N})/\text{NO}_3(\text{N})$ and $\text{NH}_3(\text{N})/\text{NO}_2(\text{N})$

VI

Figure 6: Diurnal variations in dissolved oxygen, temperature and pH and three sampling stations in the River system.





At Frankenwald Experimental farm between Stations 5 and 6 on 13th - 14th February, 1958 and 18th - 19th August 1958.

Chemical demands in ppm at 20°C are given below for August 18th - 19th.

| | | | | | | | |
|-----------|-------|------|-------|-----------|-------|------|-------|
| 1200 hrs. | 4.96 | 2400 | 14.30 | 1800 hrs. | 14.19 | 0600 | 13.79 |
| 1400 | 16.35 | 0200 | 15.26 | 2000 | 13.36 | 0800 | 15.92 |
| 1600 | 14.87 | 0400 | 14.95 | 2200 | 15.27 | 1000 | 12.95 |

At Pelindaba (Station 22) on 20th - 21st March 1958. Biochemical oxygen demands in ppm at 20°C are given below.

| | | | |
|-----------|------|------|------|
| 1200 hrs. | 1.85 | 2400 | 2.25 |
| 1600 | 2.08 | 0400 | 2.07 |
| 2000 | 4.31 | 0800 | 2.62 |

At Station 24 (Blaauwbank R.) on 5th - 6th December, 1957. A single biochemical oxygen demand is given below.

1730 hrs. 2.11 ppm.

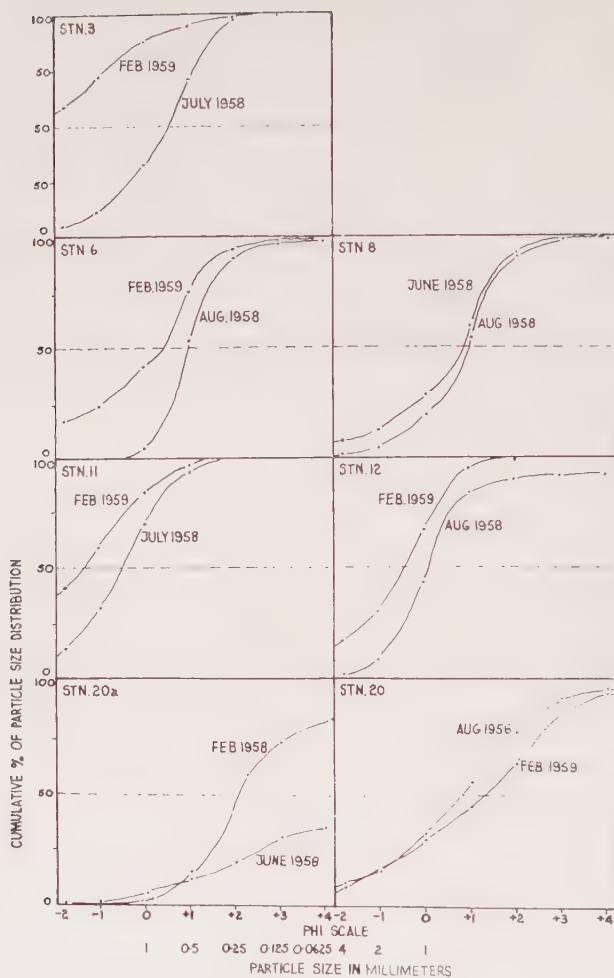


Figure 7: Phi cumulative curves for various sediments in the Jukskei - Crocodile river system during the wet and dry seasons, 1958. February - wet; June, July and August - dry.

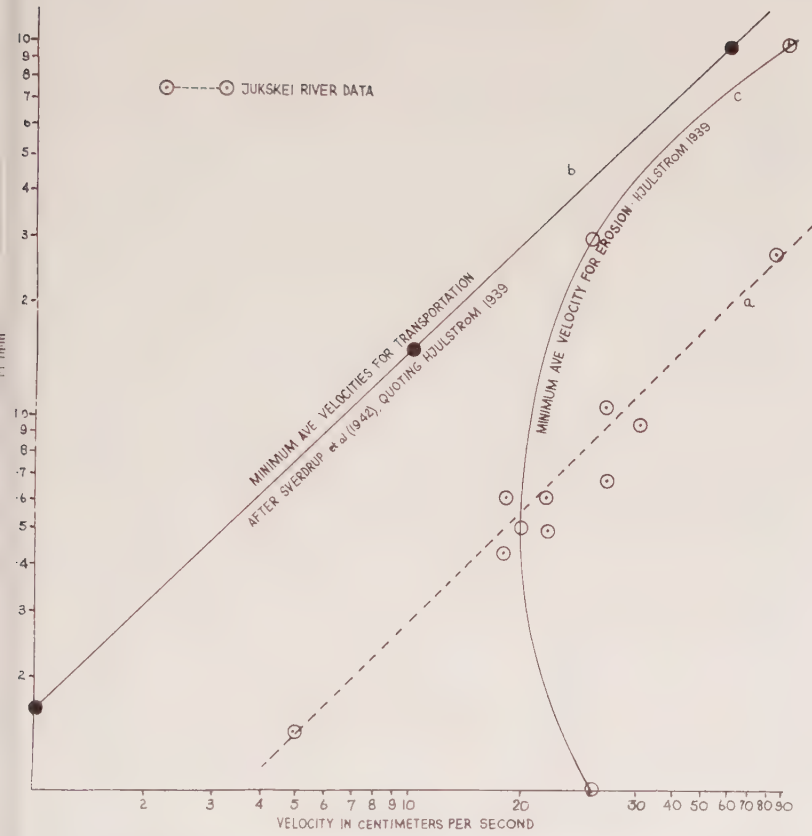


Figure 8: A logarithmic relationship between particle size (diameter) and current speed.

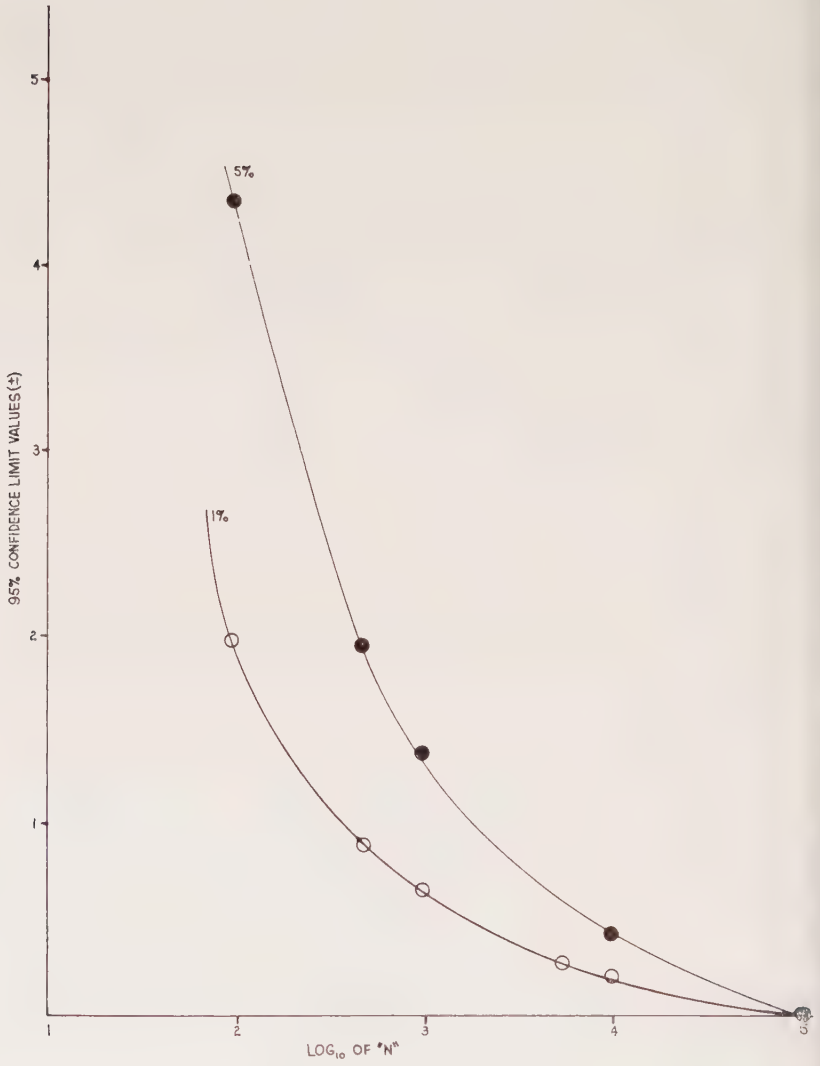


Figure 9: The effect of total sample size (N) on the 95% confidence limits of the 1% and 5% relative incidence levels.

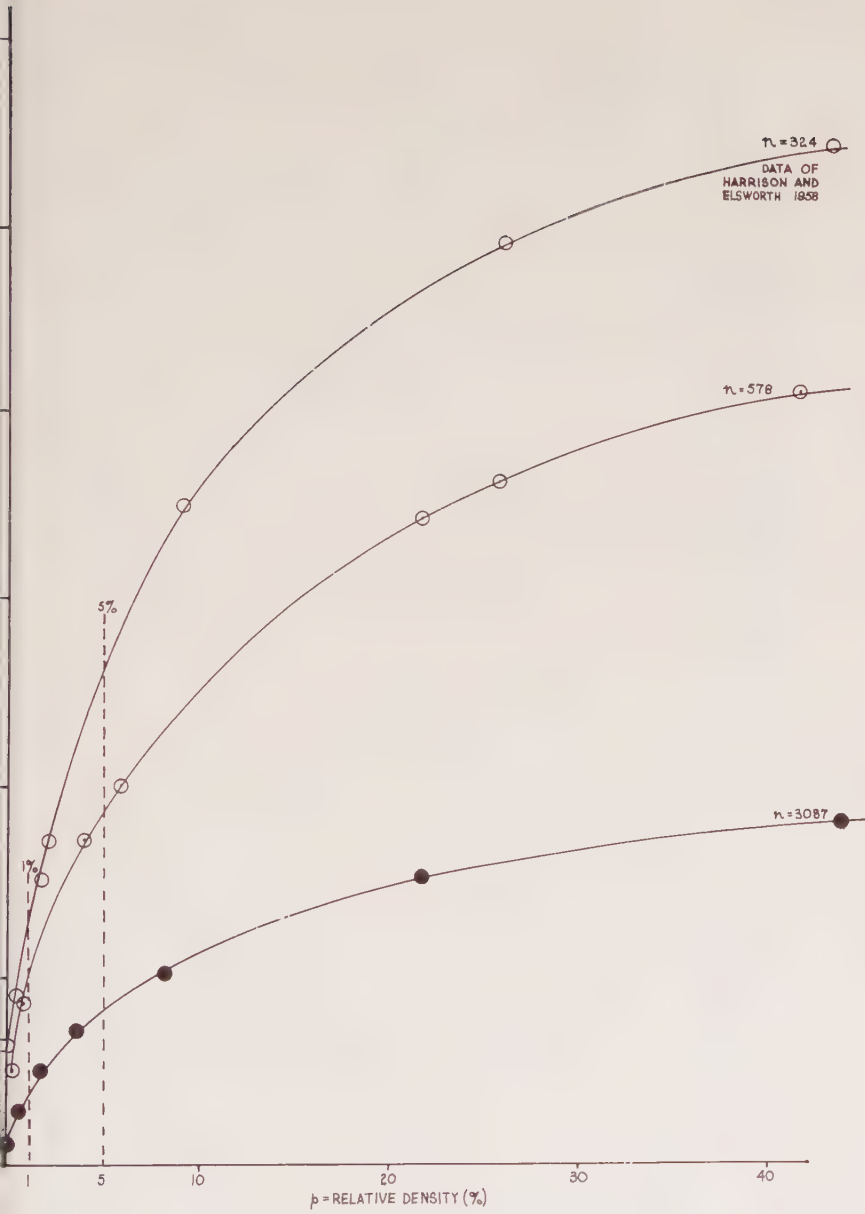


Figure 10: The effect of single sample size (n) upon the 95% confidence limits of single species proportions (p).

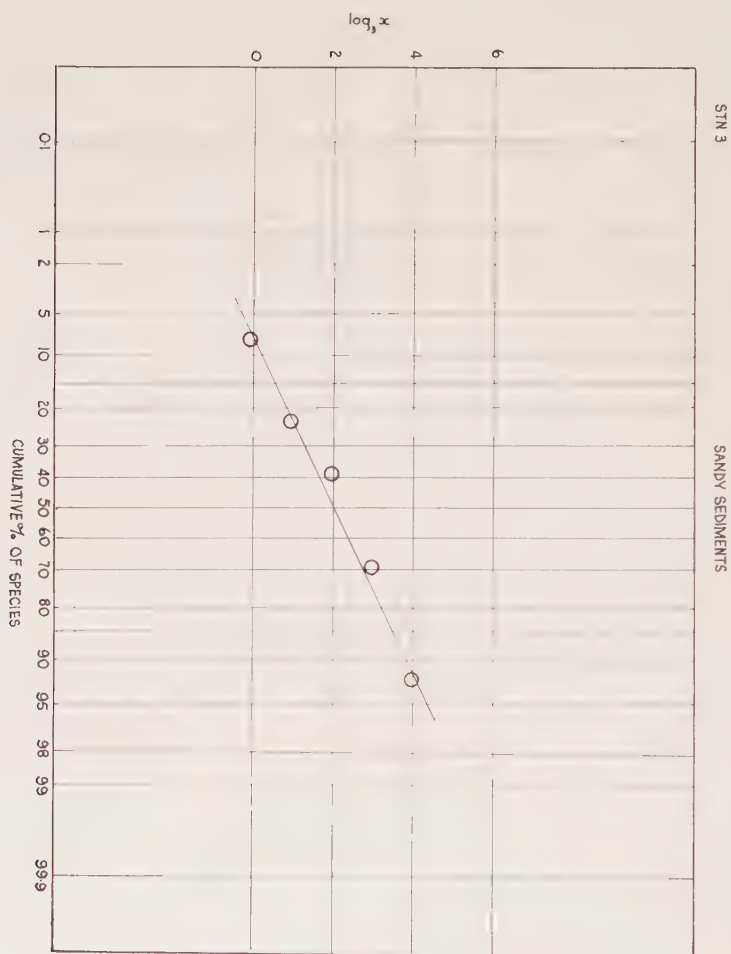
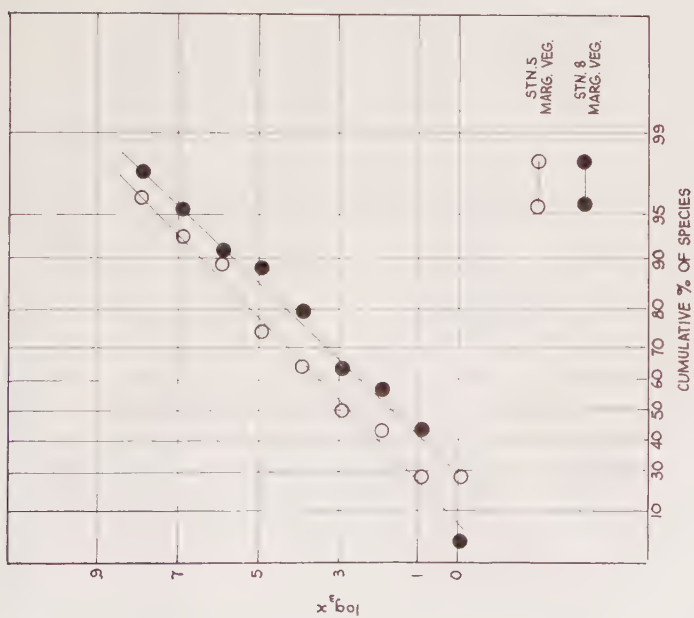
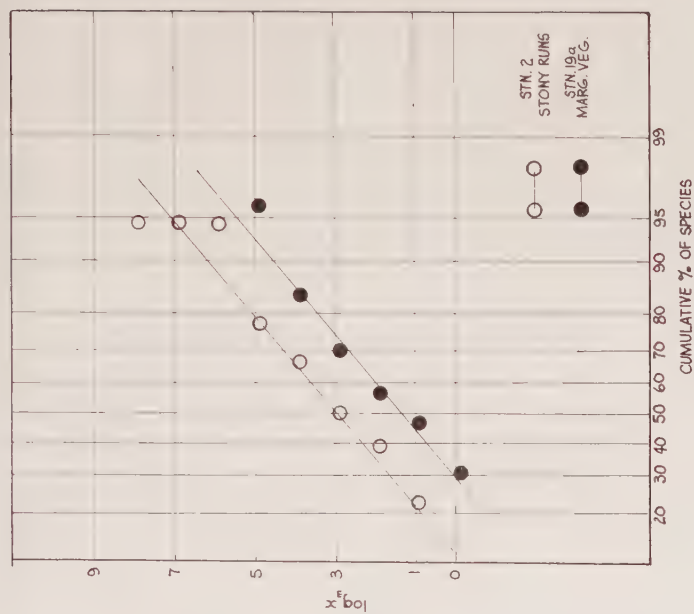


Figure 11: The fractile or probit diagrams of the proposed log - normal species - individual distributions.



The fractile or probit diagrams of the proposed log - normal species - individual distributions.

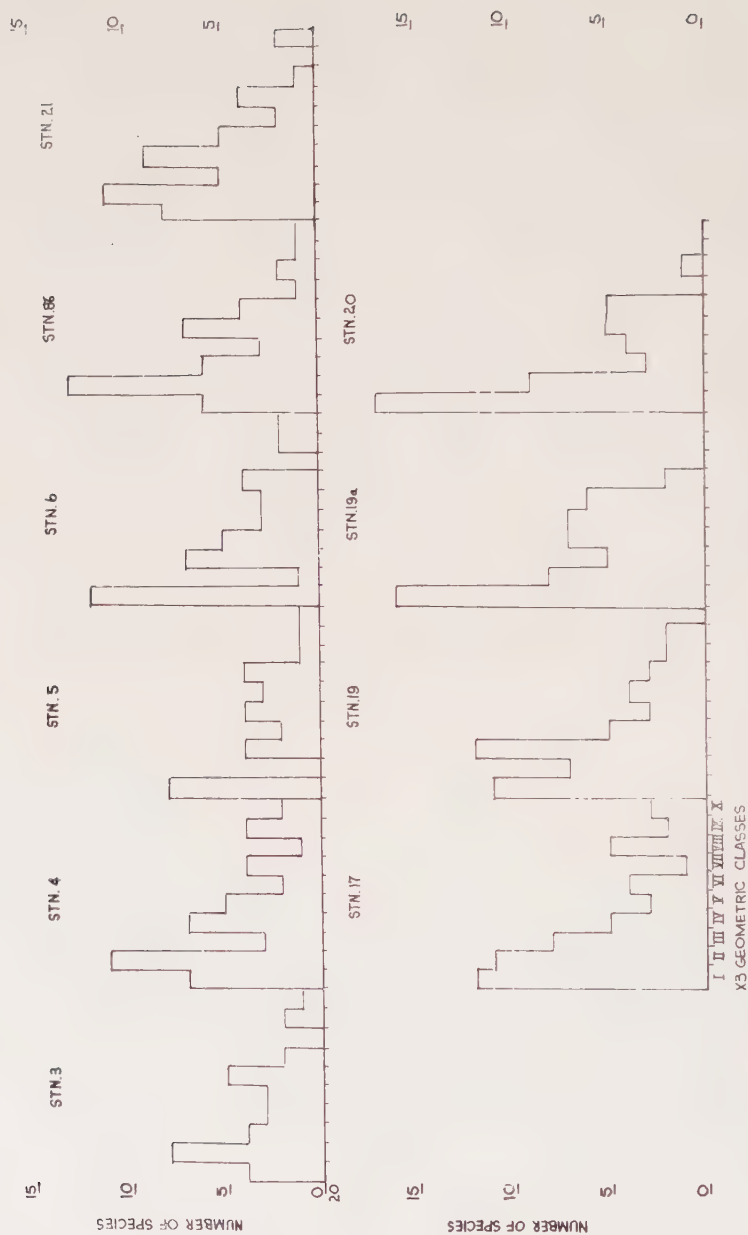


Figure 12: The species - individual distributions in the important habitats of the river system.
 a. The marginal vegetation of the Main Stream and Klein Jukskei R.

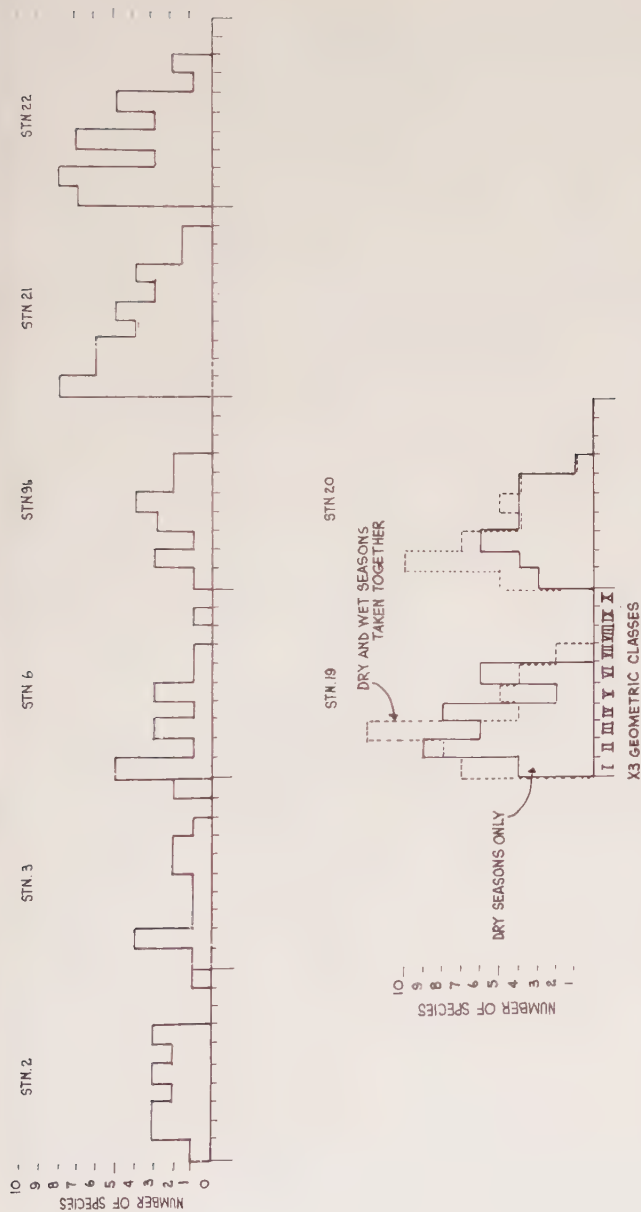


Figure 12 b: The stony runs of the Main Stream and Klein Jukskei R. based upon average numbers using a 1 sq. ft. Surber sampler.

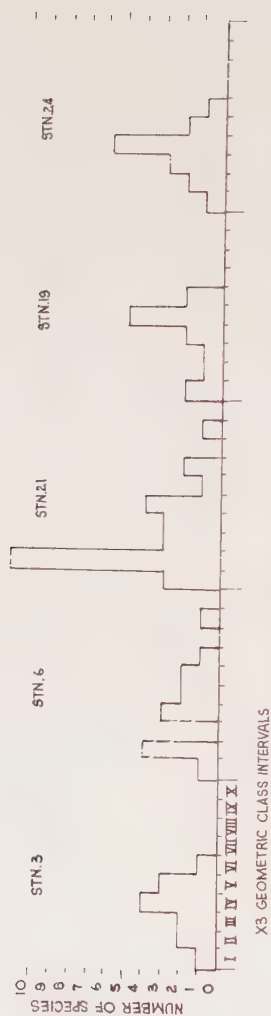


Figure 12 c: The sandy sediments of the Main Stream, Klein Juksekei R. and Blaauwbank R. The area of bottom sampled was 0.1 m^2 .

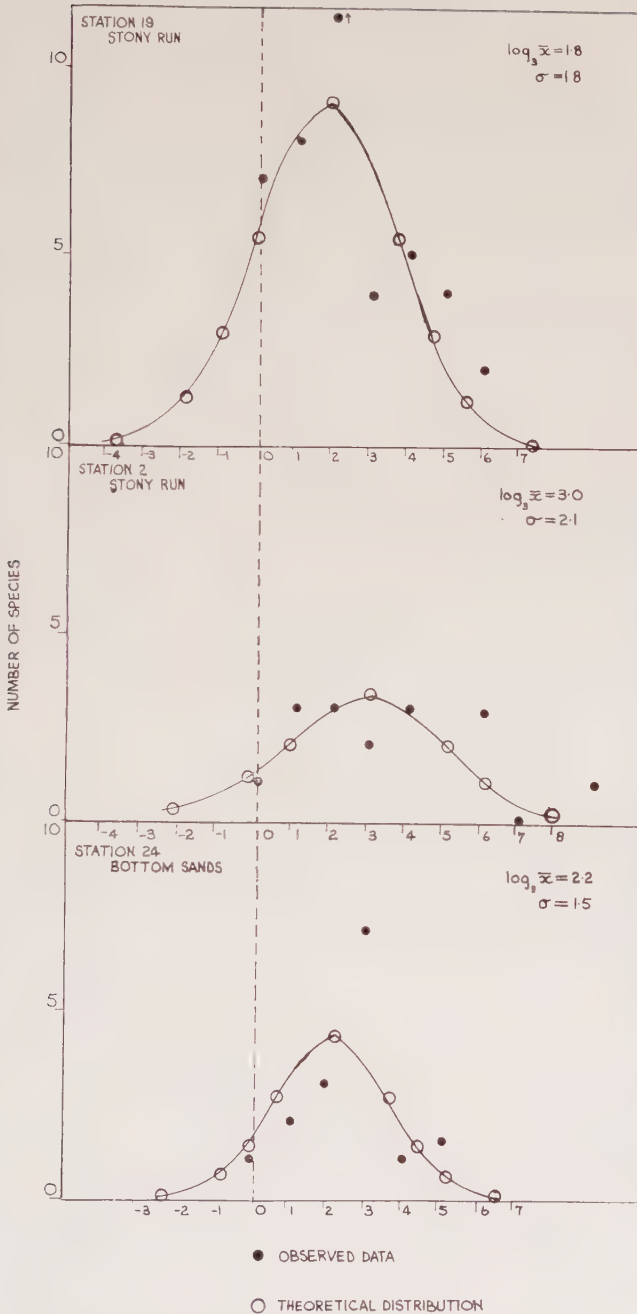


Figure 13: Fitted log-normal distributions to the observed species - individual distributions in the samples from the marginal vegetation, stony runs and sandy sediments of the Main Stream, Klein Jukskei R. and Blaauwbank R.

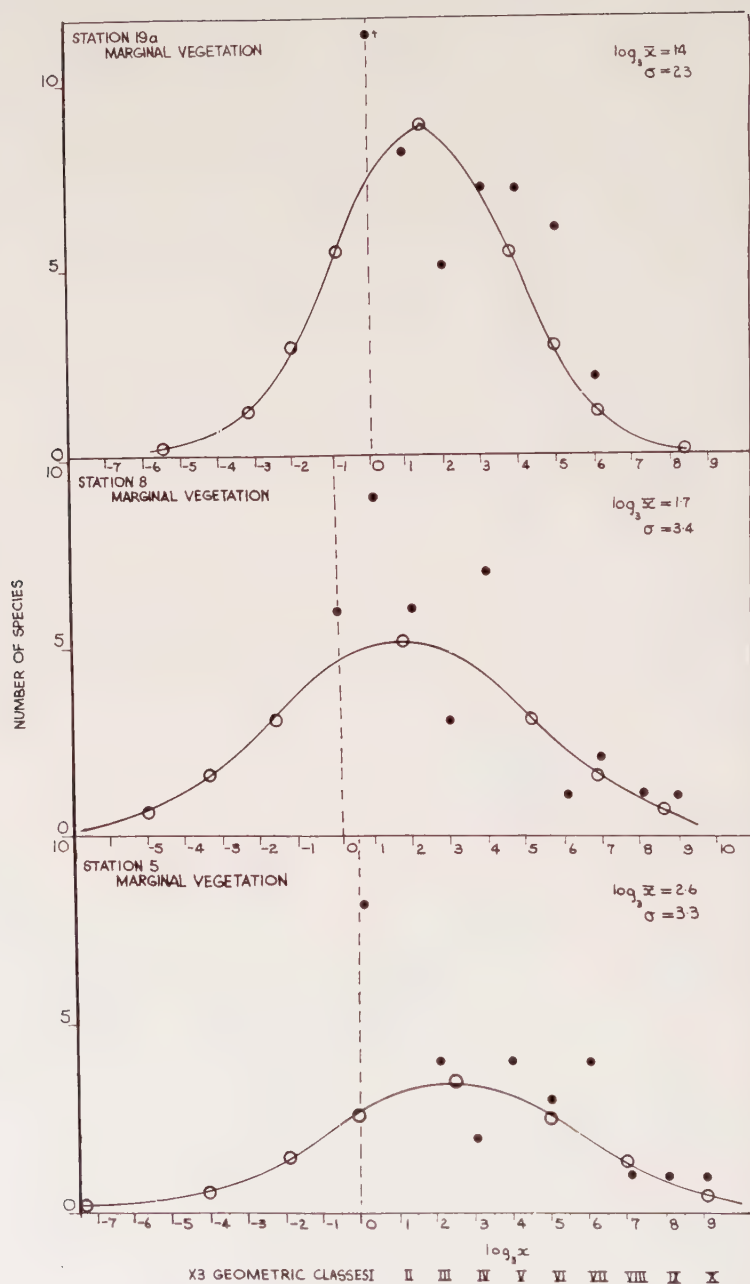


Figure 13: Fitted log - normal distributions to the observed species - individual distributions in the samples from the marginal vegetation, stony runs and sandy sediments of the Main Stream, Klein Jukskei R. and Blaauwbank R.

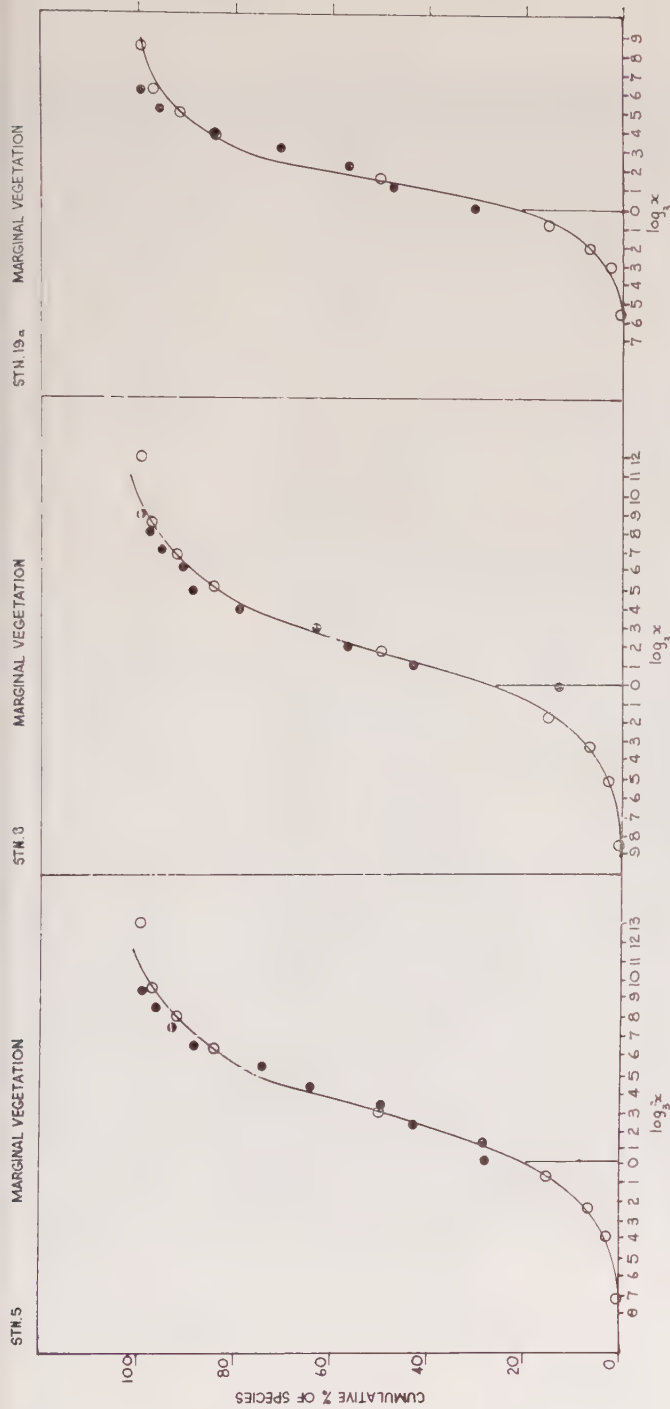
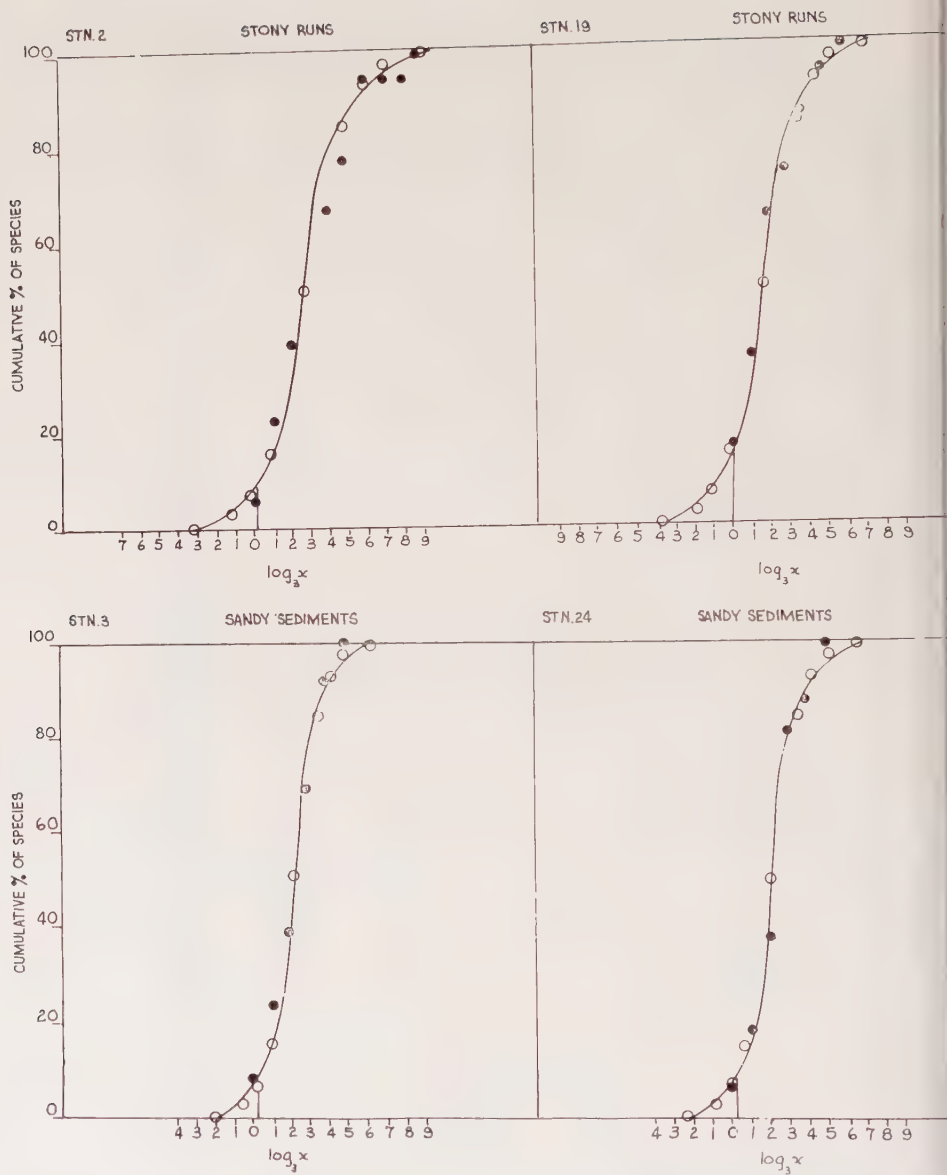


Fig. 14: Fitted cumulative distribution curves and observed cumulative polygons obtained from the species - individual distributions in the marginal vegetation, stony runs and sandy sediments of the Main Stream, Klein Jukskei R. and Blaauwbank R.



○ THEORETICAL DISTRIBUTION

● OBSERVED DATA

Figure 14: Fitted cumulative distribution curves for observed cumulative polygons obtained from the individual distributions in the marginal vegetation runs and sandy sediments of the Main Stream, Jukskei R. and Blaauwbank R.



Plate I a. Station 4 - Upper Reach



Plate I b. A portion of the Main Stream between Stations 5 and 6 and near



Plate II a. Station 8, immediately below the confluence of the Modderfontein Stream with the Jukskei R. - Middle Reach.



Plate II b. Stations 9c and 9b, the confluence of the Sandfontein and Braamfontein Streams with the Jukskei R. - Middle Reach.



Plate III a. Station 20a, immediately below the confluence of the Klein
Jukskei R. with the Jukskei R. - Middle Reach.



Plate III b. Station 21, immediately below the confluence of the Crocodile R.
with the Hennops R. - Lower Reach.



Plate IV a. Station 21 - a stony run.

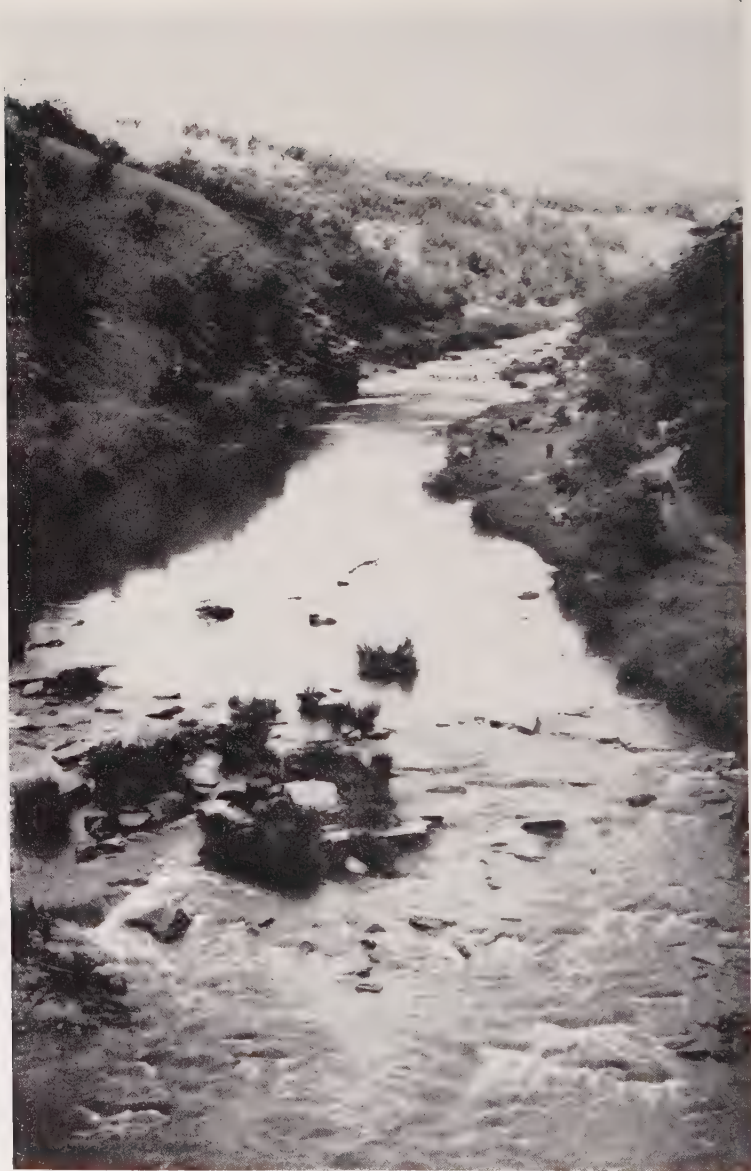


Plate IV b. Station 22. The Crocodile R., near Pelindaba - Lower Reach.

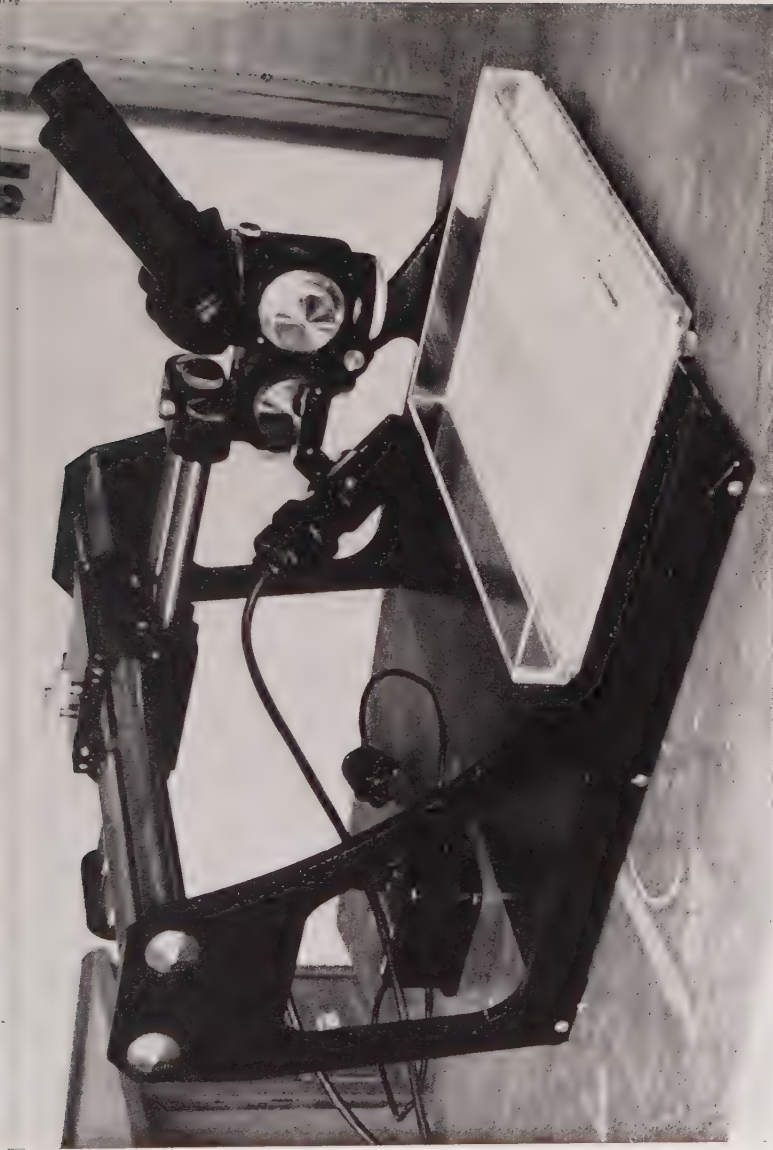


Plate V a. A scanning stand designed for use with Zeiss Stereo - Optics.



Plate V b. A typical portion of Marginal Vegetation in the Upper and Middle Reaches. The dominant plant species are *Polygonum* spp.



te VI. Synthetic detergent foam in the Jukskei River between Stations 5 and 6 at the Frankenwald Experimental Farm.
a. Detergent foam frozen of surface.



Part II

An Introduction to the
Sedimentology of Hartbeespoort Dam with
Special Reference to the Effect of
Industrial and Domestic Pollution

by

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I. INTRODUCTION

Since the total flow of the Jukskei-Crocodile River system contributed materially to the supply of Hartbeespoort Dam, it was necessary to include a study of the limnology of the dam in the authors' research programme. This was the first serious study of a water mass in South Africa and the correlated data would form a valuable contribution to our knowledge of the effects of pollution on a reservoir's catchment upon the quality of its water.

Nearly all major rivers which flow either northwards or southwards from the Witwatersrand are caught up in large irrigation reservoirs. The Union of South Africa is very poor in natural lakes and that the building and maintenance of dams has always been a primary consideration in the economic development of the country. The accent of this preliminary study has been on the physical and chemical condition of the dam. Serious zoo- and phytoplankton studies were not initiated, mainly due to the many problems that arose before the chemical and physical investigations could be carried out. However, the faunistic composition of the limited marginal vegetation is reported on, as well as investigations on the benthic fauna. During 1959—60 the dam level fell considerably and this presented an opportunity to study the effects of extended periods of drought upon the limnology of the dam.

II. DESCRIPTION OF AREA, CLIMATE AND USES

The dam (Figure 1) was completed in 1925. It was formed by the damming of the Crocodile River below its confluence with the Magalies River in a narrow gap or "poort" in the Magalies mountains, 15 miles to the west of Pretoria. When the dam is full, the shore-line is 1.5 miles, the surface area is 1500 morgen (1283 hectares) and the volume of water is estimated at 52,000 morgen-feet (13,000,000 m³), with a maximum depth of 140 feet. The dam lies in a basin of shales and diabase of the Pretoria series, at an altitude of 3,800' above sea level. It serves as a source of irrigable water for an extensive farming area to the north of the Magalies Mountains, and there is also considerable farming activity near its margins.

The main source of water is the Jukskei-Crocodile River catchment covering an area of 970 square miles; in comparison the Magalies River forms a very much smaller supply as its catchment is restricted to the east-west valley between the Daspoort and Magalies Mountain ranges.

The dam lies in an area of summer rainfall, and in the transition

between the Transvaal Highveld and Bushveld. As a result it is not subject to seasonal extremes of temperature so typical of the Highveld. The summers are hot and the winters are mild. Nonetheless the occasional snap frosts have restricted the development of warm-water fisheries in the dam, and fisheries development has been mainly restricted to more temperate water species, for example *Tilapia mossambica* and the Carp, *Cyprinus carpio*.

III. SAMPLING POINTS

The marginal vegetation was sparse and only one suitable sampling point was found, on the farm Meerhof in the vicinity of the Crocodile River inlet, Station 23. Three main open water sampling stations were chosen and are shown in Figure 1. Station 1 was situated 250 yards to the south-east of Kosmos Hill; Station 2 one mile south-west of Kosmos Hill in the Magalies River valley and Station 3 300 yards due west of the Meerhof Children's Hospital. Another Station (1a) was worked later on in this study and was directly opposite the overflow weir.

IV. VEGETATION

The marginal vegetation was restricted to a small length of shoreline. Otherwise the margins of the dam were either muddy sand or broken rubble. The marginal plant succession is shown in Figure 2, and a general view of the shore is given in Plate I. In the shallows the dominant species were *Phragmites communis*, *Polygonum lapathifolium* and *P. salicifolium*; while in deeper water, beds of *Genlisea* sp. (collection No. 1) and *Potamogeton* sp. (collection No. 2) were found in isolated clumps. During the later winter months *Polygonum lapathifolium* and *P. salicifolium* died down and were not replaced.

V. WATER BIRDS

Only two species occurred in any numbers: the Coot or Water Hen (*Fulica cristata*) and the snake bird or Cormorant (*Phalacrocorax africanus africanus*).

VI. SAMPLING METHODS

Water temperature was measured by an "Emil" -10° to 100°C thermometer; and transparency by a Secchi disc 20 cm in diameter (WELCH 1948) and estimated as the average of the readings taken at the point of downward disappearance and at the point of upward appearance. Water samples were taken with a Kemmerer sampler of conventional design from which the dissolved oxygen samples were taken by triple displacement of the Winkler bottle volume. pH was measured in the field by means of a Beckman model N meter. The bottom sediments were sampled with a Jenkin surface mud sampler. In Plate II the sampler is shown ready to be swung out and lowered at station 1. This sampler is of robust design and MUNDIE (1957) has commented favourably upon its usefulness, which this study has amply confirmed. A hand net of 25 cm diameter and mesh of 58 to the inch (0.288 mm mesh opening) was used for sampling the marginal vegetation, and a metal scoop was used to sample the muddy sands at the shore. The treatment of biological samples after collection was the same as described in Part I.

VII. ANALYTICAL METHODS

Chemical

Free water zone and bottom sediments

The analytical methods used are given in the following table: -

Water.

Dissolved oxygen: Ohle - Alsterberg modification.

OHLE, W. (1953) Die chemische und electrochemische Bestimmung des molekular gelösten Sauerstoffs der Binnengewässer. *Mitt. int. Ver. theor. Angew. Limnol.* No. 3.

ALSTERBERG, G. (1925) Methoden zur Bestimmung von im Wasser gelöstem Sauerstoff bei Gegenwart von Salpetriger Säure. *Biochem.* 2. 159, 36.

Nitrate: Sodium salicilate method.

SCHERINGA (1930) *Pharmac. Weekbl.*, 67, 362.

Nitrate: Standard Methods, American Public Health Association tenth edition. p. 153.

Phosphate: Standard methods, tenth edition. p. 169.

Sulphates: Nephelometric method.

VOSLOO, P. B. B. & D. SAMPSON (1958) The Nephelometric method for the determination of sulphate in water. *S.A. Industrial Chemist.* 12, 48.

Silicates: Standard methods, tenth edition. p. 184.

Bottom Sediments.

1. Total Carbon: WALKLEY and BLACK's rapid titration method.¹
MORGANS, J. E. C. Notes on the analysis of shallow water soft substrata
J. Anim. Ecol. 25 (2), 367—387.
2. Total Nitrogen: Kjeldahl procedure.
PERRIN (1953) *Anal. Chem.* 25, 968.
3. Sulphides: Standard methods, tenth edition. p. 274.
4. Iron: Determination of ferrous and ferric iron in iron ore.
VOGEL, A. (1958) *Quantitative Inorganic Analysis* 2nd Edition. p. 296
Longmans.
5. Copper:
KUANG, L. C. & R. H. BRAY (1953) Two specific methods of determining
copper in soil and in plant material. *Anal. Chem.* 25 (4), 655.

2. Physical.

Bottom Sediments.

A hydrometer method, originally due to BUOYOCOS and modified by MORGANS (1956), was used as the sediments were composed of particles of less than $64\ \mu$ (0.064 mm). This method, which is dependent upon STOKES' Law, gave a satisfactory estimate of the composition of the third quartile, and generated results of the following type:

| Station 1 | 2 | 3 |
|----------------|-------------------|-------------------|
| $6\ \mu$ (41%) | $10.5\ \mu$ (57%) | $17.2\ \mu$ (70%) |

These indicate, for example, at Station 1 that 41% of the subsieve had a mean diameter of $6\ \mu$. If this hydrometer method were more sensitive it would be possible to estimate the mean value in μ for the remaining 59%, and so obtain at least two values of phi in the third quartile.

VIII. RESULTS

The data reported in this section covers the period from May 1958 to September 1959.

1. The free water zone.

(a) Temperature.

From the evidence available (Figure 3) the dam is, from its temperature curves, considered as a warm monomictic lake which implies a winter circulation above 4°C . In November 1958 a classical

¹ MUNDIE (1957) cites the work of SOUTHWARD who found that ferrous iron interferes with the WALKLEY & BLACK rapid titration method for organic carbon. In Table 1, the organic carbon values are given after correction for the ferrous iron effect.

temperature curve was recorded at Station 1, and a thermocline existed between 6 m and 15 m depth. The temperature drop within the thermocline was found to be 5.7°C . The onset of the rainy season, with the accompanying flooding of the Jukskei-Crocodile river and sudden squalls of rain and wind in the dam area, effectively destroyed this classical picture, and in December (12th December 1958) was responsible for the production of 2 thermoclines and an increase in epilimnion depth (cf. RAWSON's work of the great Slave Lake, HUTCHINSON 1957). In the following summer months, up to and including March 1959, complex stratification occurred in the dam (Figure 3), and a maximum temperature curve was found in February (26.2.1959).

Although a classical thermocline was established at the onset of summer, with hypolimnetic temperature in accord with what was to be expected throughout the dam in winter, the turbulent climatic conditions were effective in increasing the temperature not only of the epilimnion, but also of the hypolimnion (cf. 26.2.59). Thus with the onset of cooler, drier and often consistently windy conditions during April hypolimnetic temperatures were closer to those of the epilimnion. The establishment of uniform thermal conditions throughout the dam occurred quite quickly; in this instance they were observed on 1.5.59 (Figure 3). Thereafter the temperature fell uniformly throughout the dam until minimum temperatures of 13.2°C at 28 m and of 13.7°C at 5 m were measured on 26.8.59. The thermal isopleths for this period are given in Figure 4 which shows nicely the rapidity of this process.

c) Secchi disc transparency.

HUTCHINSON (1957) in the summary to his chapter on the optical properties of lakes remarks that "very roughly, the light intensity at the depth of disappearance of the disk is about 5% of that at the surface and is inversely correlated with both water colour and seston content." In Figure 5 the variation in transparency is indicated by means of histograms for the three main sampling stations. The nodal transparency at Stations 1 and 2 was in August 1958 and at station 3 in July 1958. Thus, although the seasons are reversed in the southern hemisphere these results are in agreement with most European work which has shown transparency to be higher in winter than in summer. During this study there was a decrease in transparency to October 1958, followed by a marked increase in November, which was immediately followed by an equally marked fall in December, which at each sampling point became the minimum transparency recorded. The histograms indicate that maximum transparency was obtained at Station 1 while minimum transparency

was found at Station 3. At the latter station the effect of the Crocodile River was marked, and was the main cause of the decrease in transparency, particularly at the onset of the rainy season by the increase of suspended solids. An example of this is given in Plate IIIb. The water and mud core in the Jenkins sampler tube on the right was taken from Station 3 at 7 m depth, while that on the left was taken from Station 1 at 28 m.

As no direct evidence about the density of zoo- and phytoplankton was available, it was not possible to correlate the increase in transparency during November 1958 with sudden mortality of plankton blooms. However, chemical evidence obtained simultaneously with the secchi disc transparencies, indirectly supported the contention that this increase was due to a sudden disappearance of such blooms, the development of which caused the decreasing transparency between July and October 1958, particularly at Stations 1 and 2.

From these data and Hutchinson's rough rule the dam was found to have a low transparency.

(c) Dissolved oxygen.

HUTCHINSON (1957) has reviewed the more important terminology referring to the distribution of oxygen in lakes, and proposed the acceptance of ABERG and RODHE's principle terms as useful terminology. As a result of oxidative processes in the hypolimnion, this water becomes increasingly poor in oxygen until, as Figure 6 indicates for the oxygen concentrations at Station 1 during the summer of 1958—59, the oxygen curve falls off to zero. Such a distribution is termed "Clinograde". Where the oxygen concentration is uniform throughout the Dam, the curve is more or less a vertical line — a so called "orthograde" distribution. HUTCHINSON (1957) reports the work of various authors on the variations in the distribution of dissolved oxygen, especially in the region of the thermocline. Since neither a positive nor a negative heterograde distribution of dissolved oxygen was observed in Hartbeespoort Dam, the authors propose the adoption of the term "oxycline" to describe an uncomplicated fall-off towards zero of dissolved oxygen in the thermoclinical region.

During the months of November, December 1958 and February 1959, an oxycline was firmly established in the dam. Figure 6 indicates that the oxycline was steepest during February 1959 and occurred between 10 and 12 m. This data also indicates that, unlike the thermocline, the oxycline was not affected by climatic conditions, so that throughout the summer up to the early days of April the hypolimnion remained anaerobic. But, as Figure 6 indicates, the oxygen distribution in the trophic layers varied, as did the depth of the epilimnion.

Figure 6 shows the changes which took place in the clinograde oxygen distribution, which led to the breakdown of the oxycline at the onset of winter in 1959. A minimum orthograde distribution of approximately 2 ppm. dissolved oxygen was found at Station 1 on 15.5.59. The presence of this distribution confirms the conclusion, obtained from a study of temperature distribution, that complete circulation had taken place. This condition is defined by FINDENEGG (1957) as holomictic.¹ Later there occurred a rapid increase in dissolved oxygen throughout the waters of the dam; the highest orthograde concentration (5 ppm.) was measured at Station 1 on 25.5.59.

pH.

Mineral analyses for the winter of 1958 and the summer of 1958-59 are presented in Tables 10, 10a (Part 1). From this data the dam water may be defined as moderately basic. As a result the pH of the dam water was regulated by the CO_2 - bicarbonate-carbonate system. Therefore, summer increases (to pH 9) were assumed to be due to a disturbance of this equilibrium by the photosynthetic activity of planktonic algae. In this connection "marlformation" (WELCH 1952) occurred on the leaves of *Potamogeton* sp. and *Utricularia* sp. in the open water, especially during summer.

In Figure 5 surface and bottom water pH values are given for the period May 1958 to February 1959. No well defined seasonal trends are obvious, but a minimum pH was observed in the bottom waters in December at all stations. In addition, the pH of the bottom waters of the dam was generally lower than that of the surface. The range in pH is given below:

| | Surface water | Bottom water |
|-----------|---------------|--------------|
| Station 1 | 7.8—8.9 | 7.4—8.6 |
| 2 | 8.0—9.0 | 7.2—8.4 |
| 3 | 8.0—9.1 | 7.1—8.6 |

The vertical distribution of pH at Station 1 is given in Figure 7. The summer and early winter curves roughly follow the temperature and oxygen distributions in the dam. The uniformly distributed pH in May 1959 is further confirmation of complete circulation of dam water during winter.

HUTCHINSON (1957) remarks that the vertical distribution of pH

in a lake which does not undergo complete circulation and therefore remains largely or wholly unmixed was defined by FINDENEGG as meromictic. Certain very deep equatorial lakes in Africa, e.g. Lake Tanganyika, seem to fall into this category.

"will be determined by the utilization of CO_2 in the trophogenic layers and its liberation in the tropholytic, and by the possibility of the solution of bases as the CO_2 accumulates". As the waters of the dam were reasonably well buffered, mainly through its supply from the Jukskei-Crocodile River system, the pH of the hypolimnion was never observed to go below 7.0. But the marked differences between the pH of the epilimnion and of the hypolimnion in the dam indicates that the utilization of CO_2 in the epilimnion was of quite a high order.

(e) Variations in the chemical nutrients of the surface and bottom waters.

In Figures 8 and 9, seasonal variations in the concentration of phosphates ($\text{PO}_4^{''''}$), silicates (SiO_2), nitrite $\text{NO}_2(\text{N})$ and nitrate $\text{NO}_3(\text{N})$, expressed as p.p.m., are represented for the three main sampling stations during the period June 1958 to February 1959.

(i) Phosphorus.

Only the acid soluble and soluble fraction of the total phosphorus available in inland waters is reported here. This leaves quite a considerable fraction of the total phosphorus unaccounted for. The authors felt, however, that estimations of the soluble and acid soluble fraction would suffice for this preliminary study. Furthermore, it was not possible to become acquainted with the techniques for the estimation of the remaining fractions. These data must then be taken to give an estimate of soluble phosphorus and acid soluble phosphorus usually in the form of ferric and calcium phosphate.

It is well known that phytoplankton is usually a very efficient utiliser of phosphorus. In the uncontaminated lakes of the northern hemisphere the peaks of phytoplankton density usually occur in the spring turnover when phosphorus in the water is not limiting. However, during the summer in the temperate latitudes, the phosphorus concentration falls to limiting values, so that further increases of phytoplankton density are prevented, and the population usually remains in balance until the end of summer. This classical picture was not found in Hartbeespoort Dam. The high concentration of phosphorus particularly at Station 3 was clear evidence of the extensive degree of eutrophication in the dam water.

In the enriched dams in this highveld region, phytoplankton blooms occur during the hot wet summer. At the onset of winter there follows an often quite sudden mortality among the blue-green, e.g. *Microcystis aeruginosa* and *Anabaena* sp., which are the main components of these summer blooms, with often serious effects upon the fish life. These mortalities must liberate into the water

phosphorus in some form, which in Hartbeespoort Dam would count for the relatively high concentrations in the surface and bottom waters. However, the phosphorus and silica profiles suggest that, during August, September and October of 1958, there followed a period of considerable phytoplankton activity which from the silica profiles reached a peak in November 1958. That this was not directly followed by decreased phosphorus concentrations, which at each sampling point showed a clear rise over October 1958, was considered to be due to the onset of the rainy season, which, by the addition of this element via the Jukskei-Crocodile River, prevented limiting concentrations occurring during the summer. The variation in surface silicate concentrations indicate that this was probably a reasonable premise and confirms the field observations that phytoplankton blooms occurred irregularly.

b) Silica.

In the above section attention was drawn to the seasonal variations in silica, where they help the interpretation of the variations in phosphorus. It should be noted that, during the period of investigation, while the surface silica fell to a minimum (7.5 ppm.) in November 1958, a decrease of corresponding magnitude did not occur in the waters at Station 1. HUTCHINSON (1957) cites MORTIMER's and YOSHIMURA's work, which indicated that silica is usually contributed to the sediments and by the drainage water. The data available, particularly from Station 1, appears to confirm this, the drainage contribution being especially noticeable in December 1958. It is interesting to note that the surface silica concentrations obtained in the dam were similar to those obtained by YOSHIMURA for a monomictic productive lake in Japan.

c) The nitrogen content.

HUTCHINSON (1957) groups the forms of nitrogen present in lake water into five categories, of which data for only the last three, ammonia, nitrite and nitrate, are given in this paper. This was because these components of the nitrogen content had been used extensively in estimating the degree of pollution of the Jukskei-Crocodile River, and as a result they would be useful indicators of the seasonal effect this river had on the nitrogen content of the dam.

Free and saline ammonia was not detected by the methods used any time in the surface or bottom waters of the dam. In Figure 9, the seasonal variations in nitrite and nitrate N concentrations are given. The modal concentration for nitrite N and nitrate N, for surface and bottom waters, was found in October 1958 at Stations 1 and 2. At Station 3 this varied between October and December. Of

immediate significance is the very noticeable increase in nitrate N concentration from Station 1 to 2 and 2 to 3. As both Stations 2 and 3 were sited, where the effects of, firstly, the Magalies River and, secondly, the Jukskei-Crocodile River could be noticed, it is quite obvious that the nitrate N concentration in the dam was very largely affected by the inflowing rivers. Furthermore, the effect of the Jukskei-Crocodile River was more marked than that of the virtually unpolluted Magalies River. A very similar increase in concentration was obtained for nitrite N, although Stations 1 and 2 were comparable. In the following table the mean concentrations, together with the ranges observed for these two nitrogen forms, are given, which give some idea of the nitrogen loss, especially of nitrate N, in the waters of the dam which may be likened to the process of self-purification in a river.

| Stations | Surface | | Bottom. | |
|----------|---------------------|---------------------|---------------------|-------------------------|
| | NO ₂ (N) | NO ₃ (N) | NO ₂ (N) | NO ₃ (N) ppm |
| 3 | 0.01 | 1.37 | 0.00 | 1.90 |
| | 0.20 | 3.45 | 0.27 | 3.43 |
| | 0.61 | 6.80 | 0.72 | 7.27 |
| 2 | 0.00 | 0.01 | 0.92 | 1.22 |
| | 0.10 | 0.14 | 1.96 | 2.32 |
| | 0.34 | 0.50 | 0.50 | 3.20 |
| 1 | 0.01 | 1.24 | 0.01 | 0.82 |
| | 0.10 | 2.26 | 0.08 | 2.00 |
| | 0.57 | 3.25 | 0.25 | 2.68 |

It is difficult to give a precise reason for the October peak in nitrite N and nitrate N, except to say that, since the effect of the inflowing rivers was so marked, this peak should be related to some change in the chemical composition of the inflowing streams. The data given in Table 17 of Part 1 suggests that, for the dry season of 1957, the mass of nitrate and nitrite N delivered per unit time past Station 22 in the Jukskei-Crocodile River increased from May to August. Since it was our experience that effluent discharges in the catchment area had been effectively constant throughout the period of the Jukskei-Crocodile River study, and that the flow in the whole system was generally at its lowest just before the onset of the rainy season, the hypothesis is put forward that the increase concentrations of nitrate N and nitrite N in the river water due to the decreased flow were responsible for the peak concentrations in the dam at the end of the dry season in 1958.

The chemical and physical conditions of the bottom sediments.

The main chemical and physical features of the sediments from stations 1, 2 and 3 are summarised in Table 1. No important seasonal differences were observed in either total carbon, nitrogen, iron or copper. However, total carbon was somewhat higher at Station 3 and likewise total nitrogen and acid soluble phosphorus. Total iron was considerably higher in the finer sediments at Stations 1 and 2 than at Station 3. The high concentrations of copper were caused by the use of copper sulphate in an attempt to control algal growth by the irrigation authorities. Since the pH of the surface water, especially during summer, was high it was not surprising to find concentrations of this order in the sediments.

From the evidence available the proportion of ferrous iron in the sediments increased markedly from August 1958 onwards and similarly the concentration of sulphides estimated as ppm. S. These data are given in Table 1 and are in complete agreement with what could be expected in view of the anaerobic character of the hypolimnion during summer. The change in character of the sediments at station 1 is shown in Plate III a and b. The left hand core in IIIB (collected on 12.12.58) shows a thin black anaerobic layer near the surface. A complete anaerobic core is also shown (III a) which was collected from Station 1 on 22.12.59 and kept at room temperature for three days. At the end of this short period extensive gas formation had lifted the upper 2 cm of the core as can be seen in the plate. After this layer disintegrated and floated to the surface. The effectiveness of the anaerobic hypolimnion especially at water temperatures obtained in warmer climates, in rapidly converting aerobic sediments into anaerobic sediments is only too obvious.

Fauna of the marginal vegetation, sands and deep sediments.

a) The marginal vegetation at Meerhof (Station 23).

The common species of this habitat are listed in Table 2. The following species were consistently dominant throughout the investigation: -

Hydra sp.

Cyclops spp.

Hydracarina spp.

The next most important group of species was an association of *Austrocloeon virgiliae* and *Austrocloeon* sp. A. It was difficult to separate the nymphs of these species in every sample, hence the

arrangements in Table 2. The most important predators recorded were *Enallagma glaucum* and *Pseudagrion massaicum*, the nymphs of which appeared quite consistently between June 1956 and June 1957. During the summer months of 1956—57 the imago of the anisopteran, *Brachythemis leucosticta*, was often to be found flying just above the muddy shores of the dam. The nymphs of the species however, were never found in large numbers at any time during this study.

Seasonal changes in the abundance of the common species was more marked in the planktonic entomostracan, *Chydorus globosus*, which during July, August, September and October occurred in vast numbers, while the relative importance of *Pleuroxus aduncus* had fallen when compared with its incidence in the pond-like stretches of the main stream (Part 1). The change in number of *Cricotopus scottae* larvae did appear, from the data in Table 2, to follow the summer and winter alternation, with the species being more numerous in a 10' sweep of marginal vegetation during the dry winter months of June, July and August. A similar though less well defined trend was observed for *Austroclleon virgiliae*-*Austroclleon* sp. A complex and *Pseudagrion massaicum*.

The faunal composition described is representative of this habitat in the larger, moderately basic, dams of this region. The fauna is rich numerically, so offering further support to the view that the dam waters are highly productive.

(b) The fauna of the sandy bottoms.

The description of the physical and chemical condition of these sands is given in Part 1, and it suffices to record here that the sediments vary from very fine to medium on the WENTWORTH scale with a corresponding decrease in sulphide content. From the evidence available, as set out in Table 3, the fauna responded in a general way to these changes, being richer numerically and in species composition in the medium sands collected in September 1958. With this restricted data, it is only possible to note that the predominance of Chironomidae, included among which were *Tanypus guttatipennis* and *Tanytarsus nigricornis*, indicated that no serious pollution of the sediments had taken place. Faunal composition of the medium sediments in September was entirely consistent with what could be expected in view of the high productivity of the dam.

(c) The fauna of the deep sediments.

In Table 4 and its associated figure the density of the animals is given in JENKINS' cores of cross sectional area 36.3 sq. cm.

Generally speaking, the faunal composition of these cores may be divided into three categories:

Oligochaeta – mainly represented by *Limnodrilus* sp.

An assortment of Entomostraca, mainly *Eucyclops* ssp. and *Alona diaphana*.

Diptera, mainly represented by *Chaoborus microsticta*.

The histograms show a marked increase in the faunal density from Station 1 to Station 3, and possibly of greater significance the sudden increase in the number of animals at Stations 1 and 2 in November 1958, as a result of the development of the anaerobic hypolimnion. The analysis records also indicated that the bottom sediments were rich in animal detritus mainly of Cladoceran origin. In addition large numbers of ephippia were found, but it was not possible to determine whether they were viable. The variable density observed at Station 3 may have indicated the inefficiency of sampling due to the lack of randomness of animal distributions in the shallow sediments and also the effect of the flow of the Jukskei-Crocodile River.

The effectiveness of sampling will of course affect the validity of the results given. MUNDIE (1957) has assumed a random or Poisson distribution of Chironomids in the sediments of Staines South Reservoir, London. He points out that if the distribution is Poisson, then the counts from a single core may be taken as the mean, and the magnitude of this value will depend upon the number of samples required to sample a population with a known accuracy. He also maintained that it should be possible to estimate the departure from randomness of any population. His own data indicated that the Chironomid fauna of this reservoir showed high aggregation during summer but gave more even distributions during winter. (He reports a co-efficient of 0.8 during winter, and, as randomness applied to the Poisson distribution requires a co-efficient of unity, it is not unreasonable to maintain that these Chironomid populations were very nearly distributed at random).

A similar analysis of the Hartbeespoort Dam data was not possible as only single core estimates were made of the population at any given time. If, however, a random distribution of animals is accepted at Stations 1 and 2, it is reasonable to argue that the resulting means should differ significantly from each other, especially as between September and November at Station 2.

IX. DISCUSSION

The only previous published work on the limnology of this dam is a short note in HUTCHINSON et al. (1933) who described the dam as

oligotrophic, on the basis of the general chemical and biological features of its waters about 5 years after its construction. From the evidence given in this recent study it is apparent that during the past 25 years conditions in the dam have changed materially and it may now be described as very eutrophic.

Qualitative studies on the plankton diatom associations have lead CHOLNOKY (1958) to describe Hartbeespoort Dam as an oxidation pond for the effluents from Johannesburg. KELLER (1960) on the other hand has described the bacteriological quality of the dam waters in the vicinity of Station 3 as "good", and classified it "as fit for recreational purposes by any standards". The overall impression is one of a body of water which has been severely affected by the industrial expansion in its catchment area. In Europe, limnologists are agreed that a lake's evolutionary sequence takes the form of initial oligotrophy to final eutrophy. JAAG (1952, 1953) and HASLER (1947) have both drawn attention to the serious consequences of domestic drainage in hastening the final and irreversible eutrophic state. JAAG (1953) draws a parallel with Lake Lemán in Switzerland, by remarking that if, one or two million years ago, this lake had been studied by the methods at present in use, the chemical and biological condition of the lake then would have been found scarcely to differ from its present day condition. This emphasises how extremely slow is the process of natural eutrophication. The fact that this change can be brought about within a mere 25 years is an astonishing thought.

Apart from the possibility of winter fish-kills, due to the mixing of a large anaerobic hypolimnion with a narrower epilimnion at the onset of winter, a most serious result of eutrophication is the development of blooms, especially, during the summer, of blue-greens. In Hartbeespoort Dam *Microcystis aeruginosa* occurred in vast quantities during the summer of 1958—59. A further eutrophic indicator was *Oscillatoria maxima*, which was found at the height of summer. The existence of such blooms has in recent years caused a considerable number of difficulties, not the least among which was mortality among cattle which drank from this and other dams.

It is to be hoped that, as a result of this type of research, the information gained will enable the pollution of new reservoirs to be either prevented or considerably reduced.

X. CONCLUSIONS

1. Hartbeespoort Dam is eutrophic with a low transparency — a condition which has developed during the past 25 years.

2. It is monomictic with complete circulation during the winter months, often resulting in low dissolved oxygen concentrations throughout the dam.
3. The nutrient component of the water is obtained directly from the Jukskei-Crocodile River and to a lesser degree from the Magalies River.
4. Rises in pH in the epilimnion were mainly caused by the photosynthetic activity of algae in the presence of moderately basic water.
5. The bottom sediments in the deeper portion of the dam underwent rapid anaerobiasis after the establishment of a thermocline and oxycline in summer.
6. The density of the fauna in the bottom sediments decreases rapidly with the establishment of the hypolimnion.
7. The sediments are rich in iron and during summer there was an increase in the ferrous component. The soluble and acid soluble phosphorus increases in the hypolimnion after a winter minimum.
8. Silica content is comparable with productive water masses in other parts of the world.
9. The faunal associations are typical of other moderately basic and highly productive waters in the same geographical region of South Africa.

XI. ACKNOWLEDGEMENTS

The assistance and co-operation of the persons and organisations recorded in Part I is gratefully acknowledged here. The senior author is also very grateful for the help of Mr. J. M. T. M. GIESKES in developing with him the study of inland waters in the Transvaal.

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Figure 1: Hartbeespoort dam.

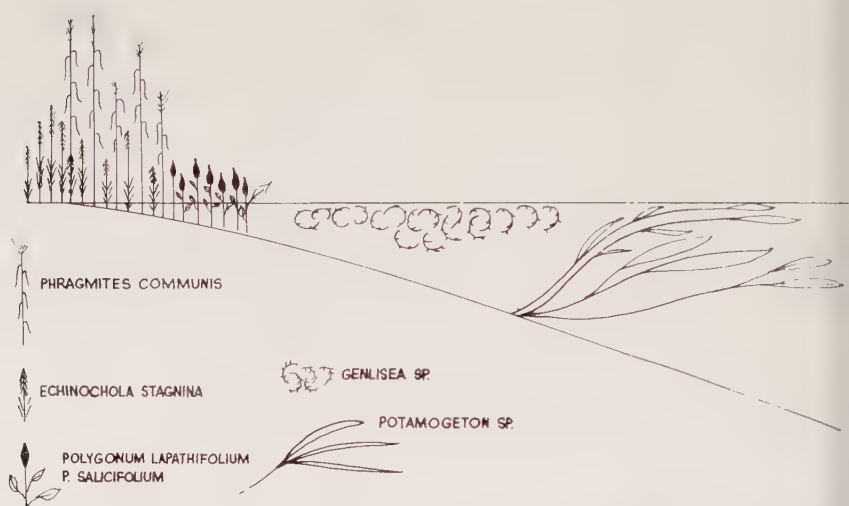


Figure 2: A schematic arrangement of the littoral vegetation at Meerhof, Station 23.

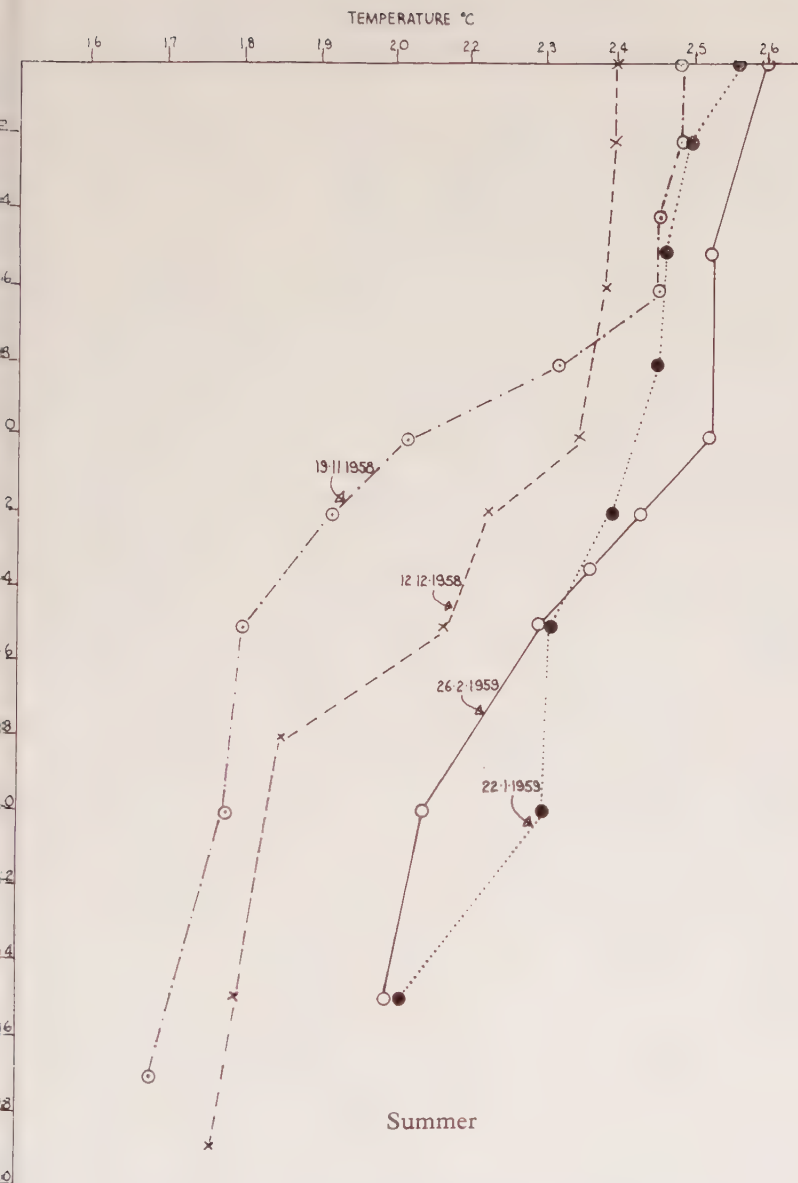


Figure 3: The vertical distribution of temperature at Station 1.

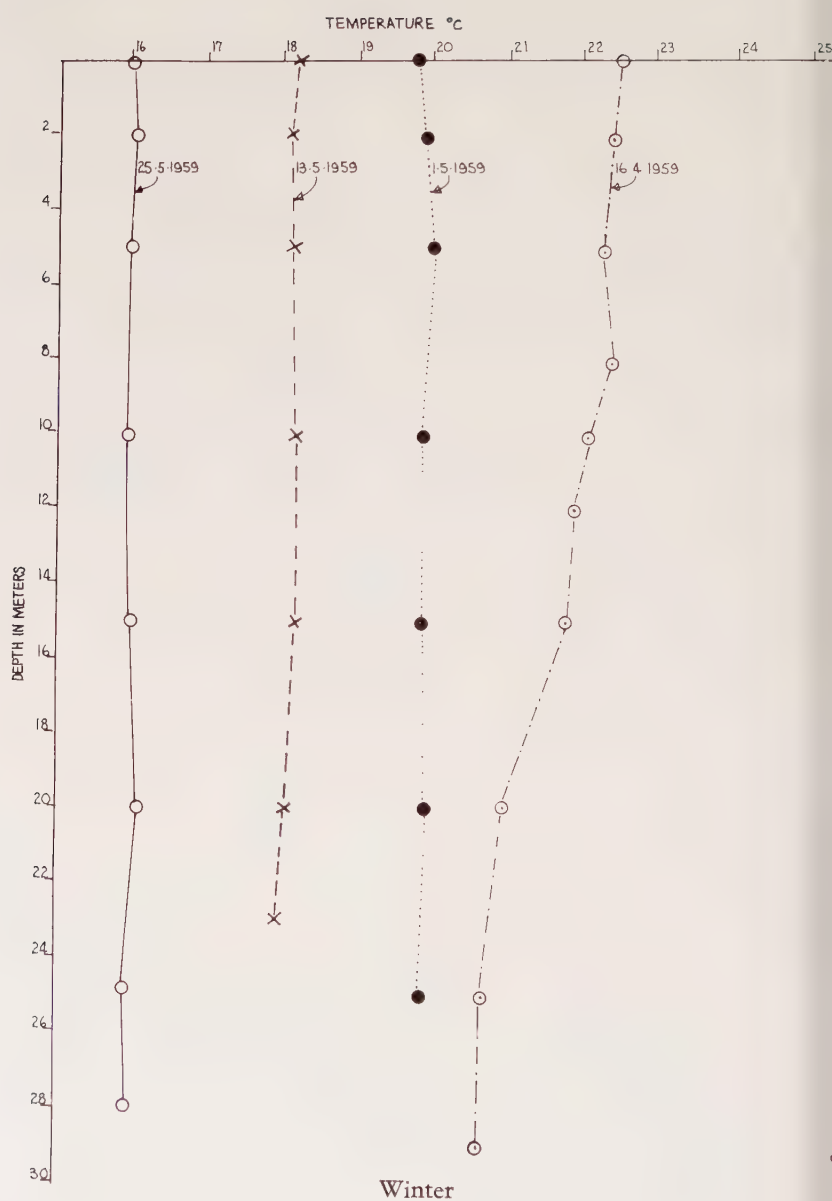


Figure 3: The vertical distribution of temperature at Station 1.

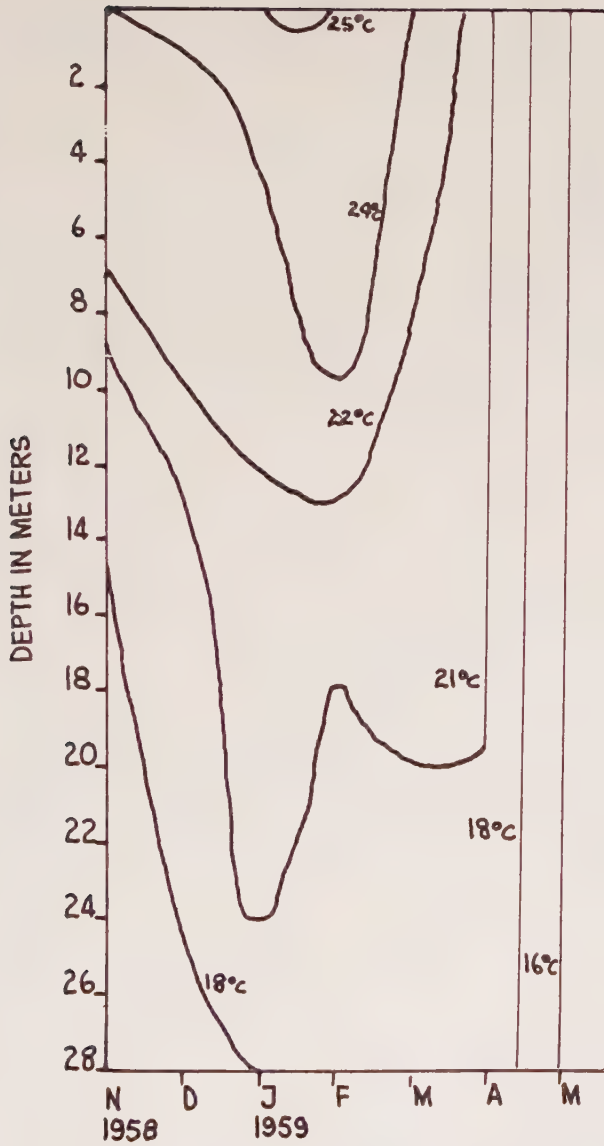


Figure 4: The thermal isopleths as measured at Station 1 during the summer and early winter of 1958—59.

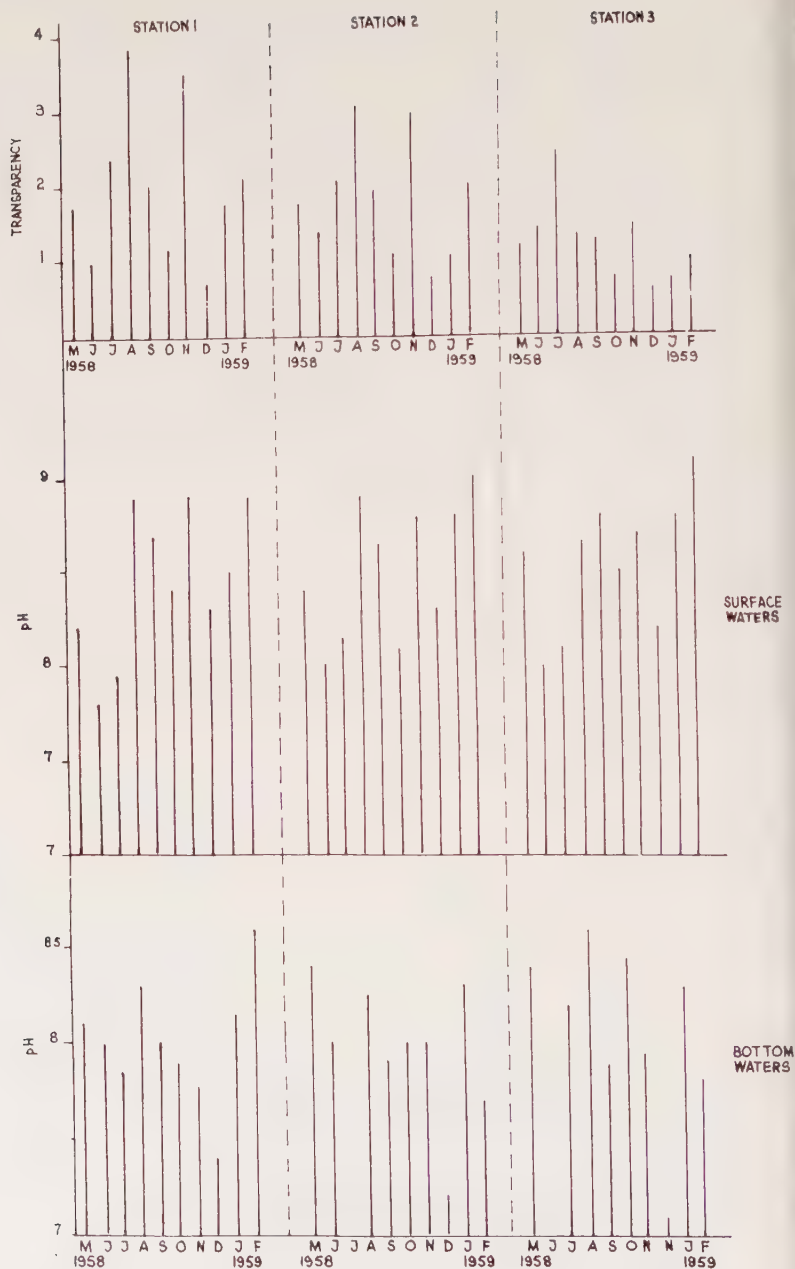


Figure 5: The seasonal variation in transparency and pH at Stations 1, 2 and 3



Figure 6: The vertical distribution of dissolved oxygen at Station 1.

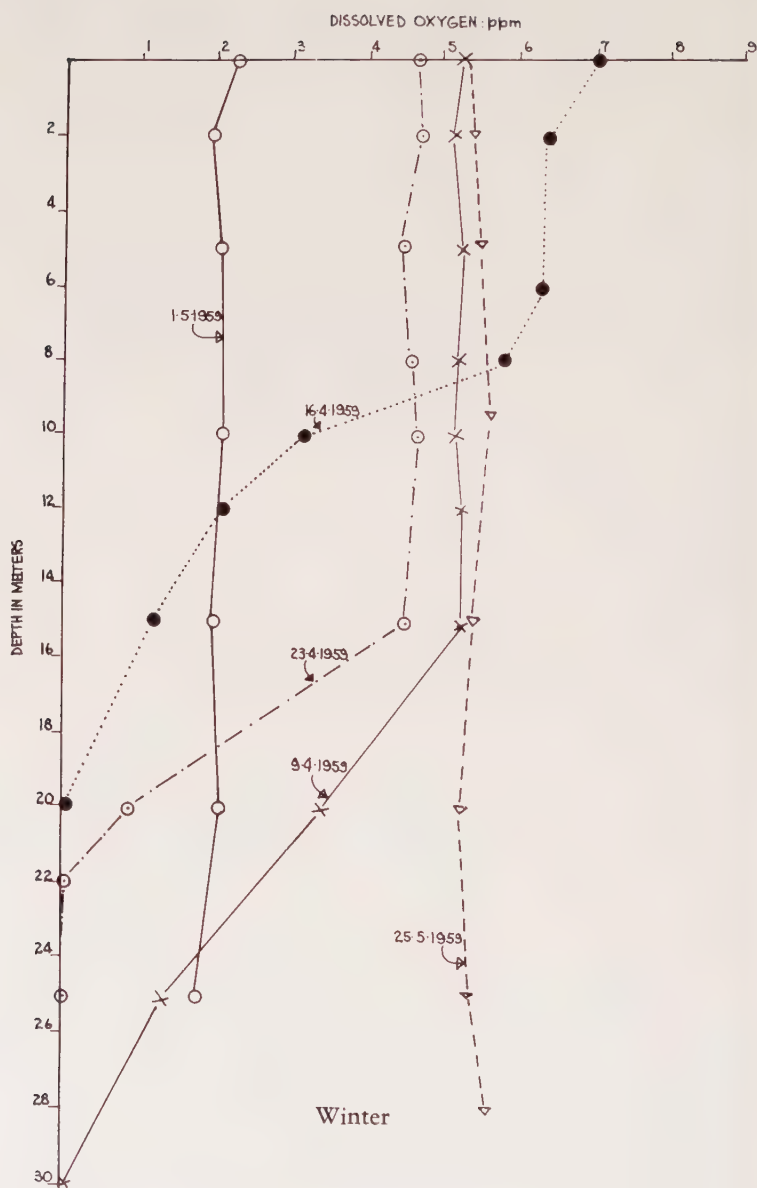


Figure 6: The vertical distribution of dissolved oxygen at Station 1.

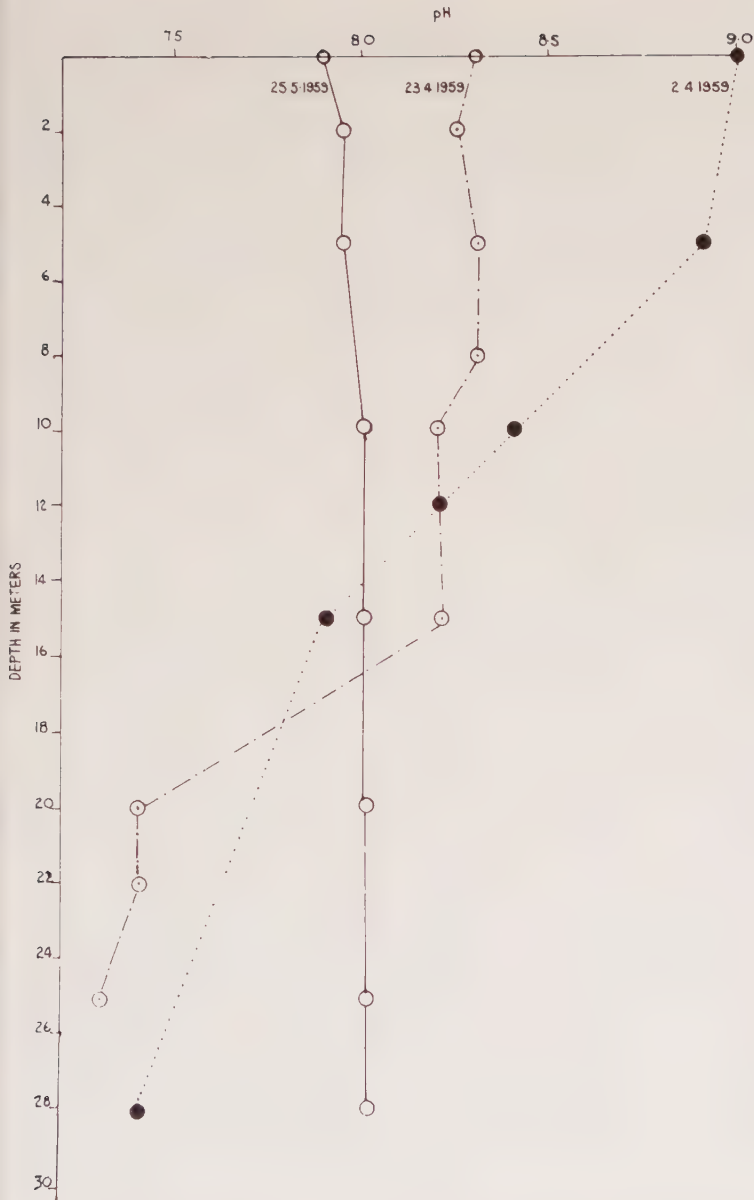


Figure 7: The vertical distribution of pH at Station 1 during late summer and early winter, 1959.

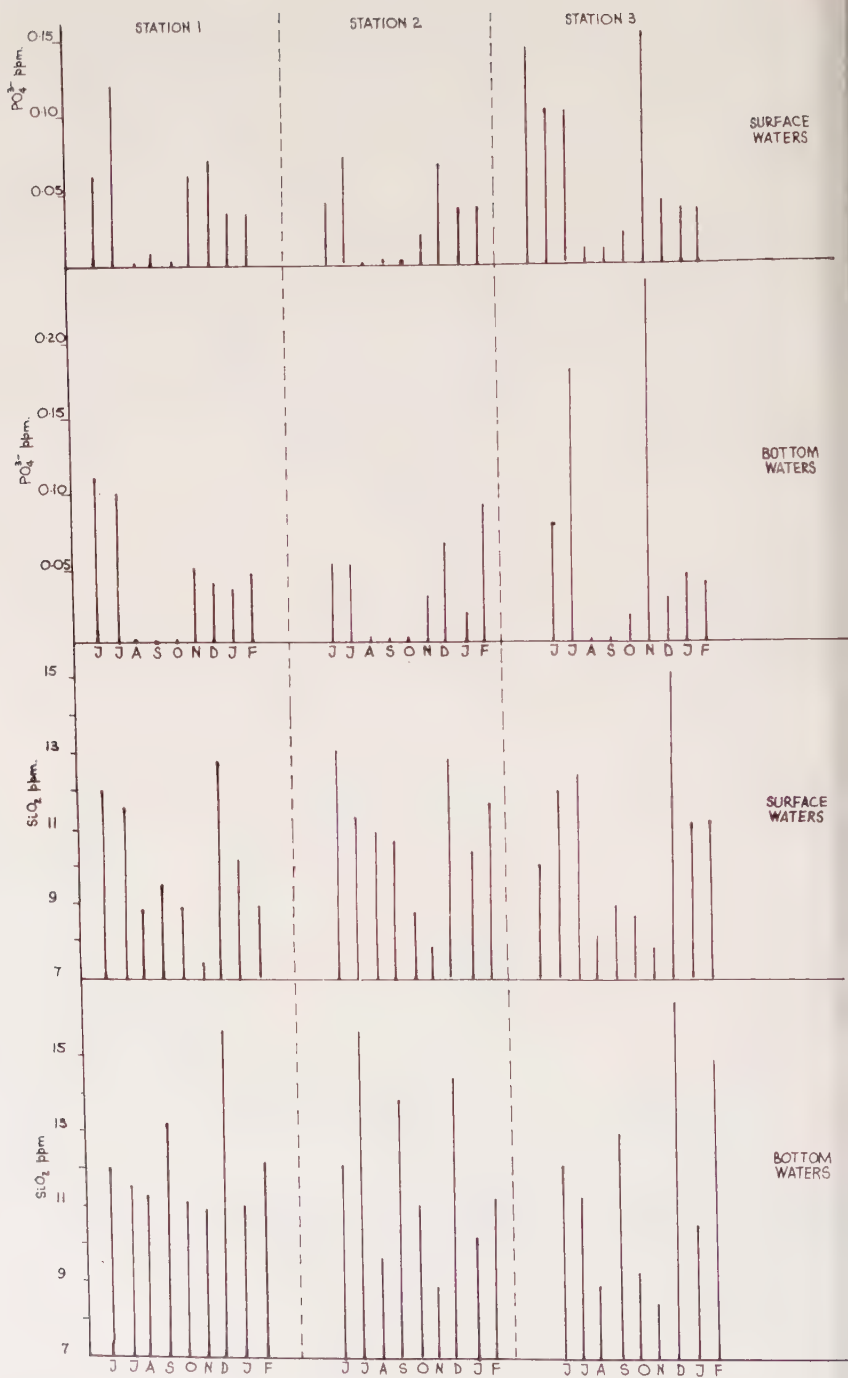


Figure 8: The seasonal variation in acid soluble and soluble phosphate and silica at Stations 1, 2 and 3.

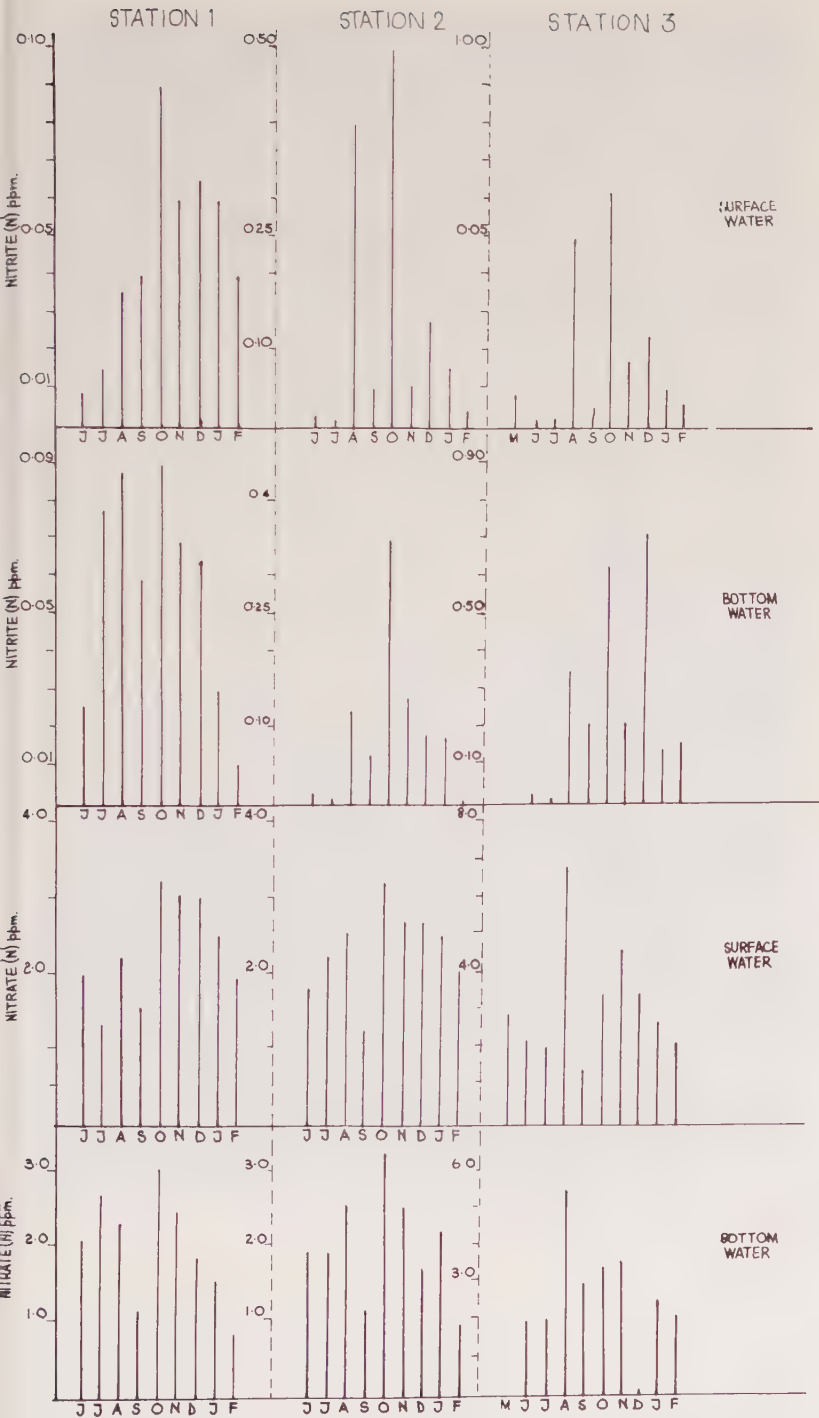


Figure 9: The seasonal variation in nitrite (N) and nitrate (N) at Stations 1, 2 and 3.



Plate 1: The Marginal vegetation at Station 23, near Meerhof during 1956—57.
One of the main components of the grasses shown was *Echinochloa stagnina*.



Plate II: A Jenkin's Core sampler ready to be lowered into the water at Station 1.

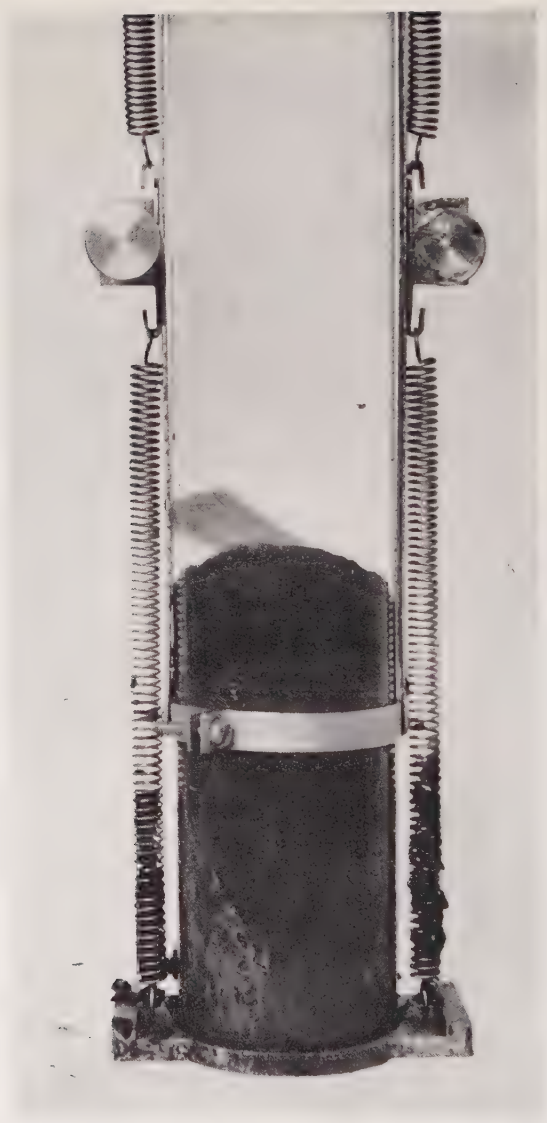


Plate III a. An anaerobic mud core collected at a depth of 23 metres at Station 1 in January, 1959.



Plate III b. Mud cores taken in January 1959 from:
 i. Bottom sediments at Station 1.

Bottom sediments at Station 3. Note the turbidity of the overlying water column.

Faune relicte sur le revers oriental du plateau de Bandiagara (Afrique occidentale)

par

J. DAGET

(avec 1 fig.)

I. LE MILIEU GÉOGRAPHIQUE¹⁾

Le plateau de Bandiagara, approximativement compris entre 14° 15' lat. N, 3° et 4° long. W, est un massif de grès primaires dominant des plaines alluvionnaires. Sa largeur ne dépasse pas 35 km à l'ouest du 14°, mais atteint 80 km plus au Nord. Vers l'Ouest, les pentes s'abaissent progressivement et plongent sous les sédiments du Tertiaire central nigérien, à une altitude d'environ 270 m. Vers l'Est, le plateau se relève et se termine brusquement par un escarpement vertical dit „Falaise” et dominant des éboulis de grès. La bordure orientale du plateau dépasse à peu près partout 450 m et atteint même 700 m à la montagne de Bamba. Au bas de la Falaise s'étend la plaine alluvieuse du Séno. Celle-ci s'abaisse assez régulièrement d'une altitude moyenne de 360 m jusqu'à la vallée du Sourou à 252 m. La partie orientale du Séno proche du plateau de Bandiagara présente des alignements de dunes faisant un angle de 55 à 65° avec le Nord. Ces dunes n'arrivent pas tout à fait jusqu'au pied de la Falaise et de ses éboulis car il existe une vallée de piedmont large de quelques dizaines de mètres à l'ouest ou quatre kilomètres.

Bien que certains indices conduisent à supposer que la Falaise est moulée sur le tracé d'une importance flexure du socle”, il est certain qu'elle ne constitue pas un miroir de faille mais qu'elle” répond à un front de côte et le plateau à son revers”. Le Séno doit alors être considéré comme „une dépression périphérique de bassin ancien du à l'érosion différentielle” et en partie comblée par

¹⁾ Pour la rédaction de ce paragraphe, nous avons fait de larges emprunts au travail de S. DAVEAU cité dans la bibliographie.

des dépôts sableux, le modelé dunaire superficiel étant évidemment d'origine éolienne.

Le plateau de Bandiagara est situé entre les isohyètes 600 et 450 mm. 75 % des pluies tombent durant les trois mois de juillet à septembre, août étant le plus arrosé; une longue saison sèche, sans aucune précipitation, dure de quatre à cinq mois. Le climat est donc très contrasté et les cours d'eau sont temporaires, sauf au voisinage immédiat de quelques sources qui conservent un débit suffisant en fin de saison sèche.

La plus grande partie du plateau est drainée vers le Niger et le Bani. Les branches maitresses de ce réseau „sont conséquentes à la fois à la pente générale du plateau et au pendage général des couches, cependant que les affluents secondaires sont visiblement sous la dépendance des fractures qui affectent les grès”. Ces rivières ont un profil longitudinal qui paraît dans l'ensemble assez régulier, bien qu'il existe parfois des rapides ou de petites chutes au passage des barres rocheuses. Il s'agit d'un réseau très anciennement constitué et qui n'a subi au cours des périodes géologiques récentes que des retouches d'ordre secondaire.

L'hydrographie du revers oriental du plateau de Bandiagara présente des caractères tout à fait différents. La zone drainée est très étroite, sa largeur étant le plus souvent de l'ordre de 1 ou 2 km, 7 ou 8 au maximum. Par conséquent les débits ne peuvent être que très faibles. Le sens d'écoulement, approximativement Nord-Sud est imposé par la direction dominante des lignes de fracture du grès. Celles-ci ont été agrandies et souvent transformées en ravins ou en gorges profondément entaillées, mais les vallées restent suspendues et ne se raccordent pas avec le niveau de piedmont. Des cascades se précipitent du haut des escarpements en saison des pluies: la plus belle, et la seule qui coule en toutes saisons, est celle de Kassa. Arrivées au bas de la Falaise, les eaux s'étalent dans la vallée du piedmont dont les parties les plus basses sont colmatées par des dépôts argileux. La seule collection d'eau permanente est la mare de Vendou. Partout ailleurs l'eau s'évapore ou s'infiltre dans les sables du Séno pour aller alimenter une nappe souterraine profonde; cette dernière n'a aucun rapport avec le Sourou, alimenté par les eaux de ruissellement superficielles et par la crue de la Volta Noire qu'un soubassement d'alluvions imperméables retient en surface. La vallée de piedmont possède quelques exutoires dirigés Nord-Ouest-Sud-Est, perpendiculaires à la direction générale de la Falaise et conséquents à la pente du Séno; telles sont les vallées de Sadia, de Guimin, de Sanga, de Diankabou. Ils entaillent les alignements dunaire sur une faible distance, une quinzaine de kilomètres au maximum puis se perdent dans les sables; ils ne se raccordent donc pas avec le

vallée du Sourou vers laquelle ils se dirigent cependant.

Pour S. DAVEAU, il s'agit d'un système hydrographique en cours d'organisation. „Les rivières empêtrées dans une masse de sable ne sont pas parvenues à la débayer et à organiser un réseau réellement hiérarchisé. Seuls les cours d'eau les mieux alimentés ont réussi à s'unir en des réseaux encore réduits à leur partie amont. Le réseau de Diankabou est le plus important de ces réseaux progressifs. Il a réussi à dégager une large vallée de piedmont où les rivières se détachent quelque peu du pied de la Falaise . . . La mise en place des sables éoliens est antérieure aux ravinements ayant excavé les vallées de piedmont et leurs exutoires. Le fait que ces derniers recoupent les alignements dunaires de la plaine montre bien qu'ils ne se sont creusés que postérieurement à la mise en place des sables et à leur modelé éolien". Par conséquent „les alignements dunaires de la plaine dateraient du dernier épisode aride auquel aurait succédé assez brusquement la période actuelle nettement plus humide". Nous verrons plus loin comment l'on peut faire cadrer ces données avec les variations climatiques du Quaternaire et l'existence d'une faune aquatique relicte dont nous allons maintenant examiner les particularités.

II. LA FAUNE AQUATIQUE

Les points d'eau permanents sur le revers oriental du plateau de Bandiagara abritent une faune aquatique dont seuls les Poissons et les Mollusques ont été systématiquement étudiés. Dans le système de la vallée de Sadia, une source pérenne naît d'une caverne de la Falaise, à 1,5 km au Sud-Ouest de Kani Kombolé. En saison des pluies, l'eau descend en cascade sur les rochers de l'éboulis et inonde une partie de la vallée de piedmont, vers 320 m d'altitude. Le 7 novembre 1959, il ne restait déjà plus qu'une petite mare, dans une dépression juste au pied de la Falaise. Cette mare, très trouble, servait d'abreuvoir aux bestiaux et contenait une grande quantité de *Clarias anguillaris*, de 90 à 100 mm de longueur standard en moyenne. Un peu plus haut, dans les creux de rochers de l'éboulis, l'eau restée claire et envahie d'Algues filamenteuses était peuplée de *Barbus pobeugini*; le plus grand individu que nous ayions récolté mesurait 52 mm de longueur standard et 62 mm de longueur totale. Ces deux points, situés au dessous du niveau de la source, s'assèchent complètement. Le 25 février 1956, S. DAVEAU rapporte n'avoir observé aucun écoulement superficiel, mais „en pénétrant dans la caverne, on se trouvait bientôt devant une étroite fissure ouverte à l'air libre vers le haut, remplie d'eau vers le bas. L'eau sourdait hors de fissures

horizontales s'enfonçant dans la masse du plateau". En fin de saison sèche, l'eau doit être encore moins abondante dans cette station et il est tout à fait remarquable que deux espèces de Poissons arrivent à s'y maintenir. Nous n'avons récolté aucun Mollusque à Kani Kombolé.

Le système de la vallée de Sanga est mieux alimenté. Depuis quelques années, un barrage, implanté dans une gorge étroite à quelques kilomètres au Sud de Sanga, a créé, vers 500 m d'altitude, une réserve d'eau qui assure un écoulement réduit mais permanent durant la saison sèche. En aval de ce barrage, la rivière s'enfonce de plus en plus profondément dans le massif rocheux puis elle „perce d'un parcours souterrain de quelques centaines de mètres les dernières épaisseurs de grès qui la séparent de la vallée de piedmont. Au dessus de ce cours souterrain, un énorme cube d'une soixantaine de mètres de côté s'est effondré d'une vingtaine de mètres entre deux cassures verticales parallèles". La construction du barrage de Sanga avait pour but principal d'assurer les besoins en eau de la population et de permettre la culture des oignons dans des jardins en terrasse faits de terre rapportée sur les entablements gréseux. Secondairement elle a permis à la faune aquatique autochtone de se développer considérablement, les conditions de vie qui lui sont offertes maintenant étant beaucoup plus favorables que celles qui existaient naturellement. La fauna locale comprenait trois espèces de Poissons: *Barbus ablakes*, *B. pobeguini* et *Clarias anguillaris*. De plus, en vue d'apporter des ressources alimentaires aux habitants, *Tilapia galilaea* a été introduit dans la retenue d'eau et y constitue maintenant l'espèce dominante. Il aurait peut-être été préférable de faire appel à *Tilapia melanopleura*, compte tenue de la présence d'une abondante végétation aquatique. Quoiqu'il en soit, et sans doute fortuitement, on a reconstitué à Sanga l'association d'espèces que l'on rencontre à la guelta de Molomhar dans l'Adrar mauritanien. Ce point d'eau abrite en effet une faune relictive de Poissons composée de *Barbus deserti*, *B. pobeguini*, *Clarias senegalensis* et *Tilapia galilaea*¹⁾. Quant aux Mollusques, ils présentent à Sanga une variété et une abondance d'individus assez inattendues dans un massif de grès. Nous y avons récolté de nombreux exemplaires de *Spathopsis rubens*, *Aspatharia* sp., *Sphaerium courteti*, *Lanistes guinaicus*, *Limnaea natalensis*, *Biomphalaria pfeifferi gaudi*, *Gyraulus fouladougouensis*, *Bulinus* sp.

Le système de la vallée de Diankabou est plus complexe. Une source pérenne jaillit du grès à Kassa, vers 500 m d'altitude. Le ruisseau qu'elle alimente traverse d'abord des jardins dans une petite

¹⁾ Les *Barbus deserti* de Mauritanie ne sont pas, d'après nous, spécifiquement distincts de *B. ablakes* et *Clarias senegalensis* diffère très peu de *C. anguillaris*.

vallée suspendue en bordure de la Falaise, puis franchit une barre de roches dures par une cascade. Celle-ci s'évaporerait parfois en cours de chute vers la fin de la saison sèche, mais le 12 mai 1960 nous l'avons trouvée encore active. La vasque de réception, au fond d'un petit cirque, est assez vaste et paraît profonde. Son trop-plein s'écoule dans des éboulis de rochers et descend vers la vallée de piedmont. En saison sèche, l'eau ne tarde pas à se perdre dans les sables; mais, lorsque le débit de la cascade est suffisant, elle va d'abord remplir la mare permanente de Vendou, puis de là se répand dans une partie de la vallée de piedmont. Le 5 novembre 1959, nous avons encore trouvé des Poissons dans les bas-fonds inondés au pied de la montagne de Bamba. La mare de Vendou, située vers 300 m d'altitude, est un fond de cuvette sableuse, colmaté par des dépôts argileux qui retiennent l'eau en surface. Ses rives sont en pente très douce de sorte que sa superficie varie beaucoup suivant les saisons. Le 13 mai 1960, sa profondeur ne dépassait en aucun point 1,50 m. Une abondante végétation aquatique, comprenant notamment *Nymphaea lotus* et *Ceratophyllum demersum*, s'y développe; le fond est recouvert d'une épaisse vase molle. Cette mare est sans doute en voie de comblement et vouée à disparaître dans un avenir plus ou moins proche. Cette éventualité ne serait cependant pas imminente dans les conditions de morphogenèse actuelle. Les rives sont fixées par la végétation, les eaux qui descendent de Kassa charrient peu de sédiment et les transports éoliens sont très limités. Cependant l'érosion des terres cultivées dans la vallée de piedmont et la mobilisation des sols par le piétinement du bétail, le surpâturage étant fréquent près des points d'eau, peuvent accélérer le comblement.

En aval de la cascade de Kassa, nous avons identifié dix espèces de Poissons: *Gnathonemus senegalensis*, *Alestes nurse*, *Barbus ablabes*, *B. pobeguini*, *Chrysichthys walkeri*, *Synodontis schall*, *Clarias anguillaris*, *Heterobranchus longifilis*, *Hemichromis bimaculatus* et *Ctenopoma kingsleyae*. Si l'on classe ces espèces en soudaniennes, guinéennes et indifférentes, comme nous l'avons fait pour la faune des bassins de la Volta Noire et de la Haute Comoé par exemple (DAGET, 1960), on trouve la répartition suivante: 30 % de soudaniennes, 40 % de guinéennes et 30 % d'indifférentes. Sous cette latitude et avec le climat actuel, la légère prédominance des formes guinéennes peut s'expliquer dans des milieux essentiellement rocheux comme la vasque de réception de la cascade de Kassa et le défluent qui s'en échappe. Par contre, dans un biotope typiquement soudanien comme la mare de Vendou, elle indique un déséquilibre et un manque d'adaptation de la faune. Sur le plan pratique, ceci se traduit par une production piscicole anormalement faible. Chaque année, aux basses eaux, quelques pêcheurs professionnels viennent à la mare de Vendou;

ils n'y capturent que des *Clarias anguillaris* de 4 à 500 mm de longueur standard, à l'aide de lignes à hameçons multiples posées le soir et relevées le lendemain matin. Les autres espèces sont de trop petite taille ou trop peu nombreuses en individus pour être exploitées. Il est certain que la végétation aquatique qui encombre actuellement les eaux rend impossibles l'usage des filets et une exploitation totale du stock de Poissons; mais l'introduction de certaines espèces choisies de façon à utiliser tous les niveaux alimentaires relèverait notablement la productivité de la mare de Vendou. Un herbivore comme *Tilapia melanopleura* ou *T. zillii*, un planctonophage comme *Tilapia nilotica*, un microphage à croissance rapide comme *Heterotis niloticus*, un prédateur facile à contrôler comme *Parophiocephalus obscurus*, devraient bien prospérer dans un tel milieu.

Au dessus de la cascade de Kassa, nous n'avons trouvé que quatre des dix espèces qui existent en aval: *Barbus ablakes*, *B. pobeguini*, *Clarias anguillaris* et *Hemichromis bimaculatus*. En fin de saison sèche, le débit de la source étant réduit, ces Poissons se réfugient dans des anfractuosités et des trous de rochers qui restent remplis d'eau mais pas toujours en communication avec le ruisseau. Les contenus stomacaux de plusieurs *Barbus ablakes*, *B. pobeguini* et *Hemichromis bimaculatus*, capturés le 13 mai 1960 dans ces biotopes, ont été examinés: ils donnent une idée de la variété sinon de l'abondance des ressources alimentaires utilisées par ces Poissons. Les *Barbus pobeguini* ont fourni surtout du phytoplancton et quelques Ostracodes, les *B. ablakes* une forte proportion de phytoplancton mais aussi des débris d'Insectes, de Mollusques, des Ostracodes et quelques soies d'Oligochètes, les *Hemichromis bimaculatus* surtout des débris d'Insectes (Coléoptères, larves de Chironomides), des Cladocères, des Ostracodes, quelques Copépodes, des débris de Mollusques et quelques Algues. Quant au phytoplancton il comprenait des Chlorophycées (*Spyrogira*, *Oedogonium*), des Desmidiées (*Closterium*, *Cosmarium*), des Diatomées (*Navicula*, *Amphora*, *Synedra*, *Melosira*, *Cyclotella*) et des Cyanophycées.

Les Mollusques sont plus rares qu'à Sanga. Nous avons récolté *Limnaea natalensis* et *Biomphalaria pfeifferi gaudi* en haut de la cascade de Kassa, *Lanistes guinaicus* et des restes de Lamellibranches indéterminables en aval.

La faune aquatique autochtone du revers oriental du plateau de Bandiagare, très réduite à Kani Kombolé, plus riche particulièrement en Mollusques à Sanga et en Poissons à Kassa, comprend les espèces suivantes:

| Poissons | Kani Kombolé | Sanga | Kassa |
|--|--------------|-------|-------|
| <i>Gnathonemus senegalensis</i> (STEINDACHNER) | | | × |
| <i>Alestes nurse</i> (RÜPPELL) | | | × |
| <i>Barbus ablables</i> (BLEEKER) | | × | × |
| <i>Barbus pobeguini</i> PELLEGRIN | × | × | × |
| <i>Chrysichthys walkeri</i> GÜNTHER | | | × |
| <i>Synodontis schall</i> (BLOCH SCHNEIDER) | | | × |
| <i>Clarias anguillaris</i> (LINNÉ) | × | × | × |
| <i>Heterobranchus longifilis</i> C. et V. | | | × |
| <i>Hemichromis bimaculatus</i> GILL | | | × |
| <i>Ctenopoma kingsleyae</i> GÜNTHER | | | × |
| Total | 2 | 3 | 10 |
| Mollusques | | | |
| <i>Spathopsis rubens</i> (LAMARCK) | | × | |
| <i>Aspatharia</i> sp. | | × | |
| <i>Sphaerium courteti</i> GERMAIN | | × | |
| <i>Lanistes guinaicus</i> (LAMARCK) | | × | × |
| <i>Limnaea natalensis</i> KRAUSS | | × | × |
| <i>Biomphalaria pfeifferi gaudi</i> (RANSON) | | × | × |
| <i>Gyraulus fouladougouensis</i> GERMAIN | | × | |
| <i>Bulinus</i> sp. | | × | |
| Total | 0 | 8 | 3 |

III. AFFINITÉS DE CETTE FAUNE

Les *Alestes nurse*, *Barbus ablables*, *B. pobeguini*, *Synodontis schall*, *Clarias anguillaris*, *Heterobranchus longifilis* et *Hemichromis bimaculatus* que nous avons récoltés sur le revers oriental du plateau de Bandiagara ne diffèrent apparemment en rien de ceux du Niger ni de ceux de la Volta. Sur sept *Clarias anguillaris* provenant de Kani Kombolé et Kassa, nous avons trouvé les nombres de rayons et de branchiostyles suivants :

| Nombres de rayons à la dorsale | | | | | | | | | | | |
|--------------------------------|----|----|----|----|----|----|----|----|----|----|--|
| | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | |
| Fréquence | 1 | | | | 2 | 1 | 1 | | 1 | 1 | |

| Nombres de rayons à l'anale | | | | | | | | | |
|-----------------------------|----|----|----|----|----|----|----|----|--|
| | 52 | 53 | 54 | 56 | 56 | 57 | 58 | 59 | |
| Fréquence | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | |

| Longueur standard | Nombre de branchiospines
au 1er arc branchial | |
|-------------------|--|--|
| 85 mm | 17 + 3 = 20 | |
| 93 | 20 + 3 = 23 | |
| 94 | 18 + 2 = 20 | |
| 98 | 17 + 3 = 20 | |
| 100 | 18 + 2 = 20 | |
| 105 | 18 + 3 = 21 | |
| 110 | 18 + 2 = 20 | |

Gnathonemus senegalensis existe aussi dans le bassin du Niger et dans celui de la Volta; mais les populations de la zone d'inondation du Moyen Niger constituent une sous-espèce distincte, *G. s. elongatus* (PFAFF), dont les populations voltaïques diffèrent par un nombre de rayons plus faible aux nageoires dorsale et surtout anale. A ce point de vue, les *G. senegalensis* de Kassa se rapprochent davantage de ceux de la Volta que de la sous-espèce nigérienne, comme le montre le tableau suivant où figurent les nombres que nous avons relevés sur 27 *G. senegalensis* de Kassa, 30 du bassin de la Volta Noire et 75 *G. s. elongatus* de la zone d'inondation du Moyen Niger:

| Nombres de rayons à la dorsale | | | | | | |
|--------------------------------|----|----|----|----|----|--|
| | 26 | 27 | 28 | 29 | 30 | |
| Fréquence { | 7 | 9 | 6 | 4 | 1 | |
| | 15 | 10 | 5 | | | |
| | 7 | 15 | 20 | 23 | 10 | |

| Nombres de rayons à l'anale | | | | | | | | | | | |
|-----------------------------|----|----|----|----|----|----|----|----|----|--|--|
| | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | | |
| Fréquence { | 1 | 1 | 9 | 10 | 5 | 1 | | | | | |
| | | 4 | 16 | 7 | 3 | | | | | | |
| | | | 2 | 6 | 18 | 26 | 17 | 5 | 1 | | |

Chrysichthys walkeri et *Ctenopoma kingsleyae* existent dans le bassin de la Volta, mais n'ont pas été trouvés dans celui du Moyen Niger où

C. kingsleyae est remplacé par *C. petherici*. Nous avons montré (DAGET, 1958) combien ces deux espèces sont morphologiquement proches l'une de l'autre et comment on peut les distinguer par les moyennes des nombres d'épines dorsales et anales, respectivement supérieures chez *C. petherici* et inférieures chez *C. kingsleyae* à 17,60 et 9,30. Nous avons comparé à ce point de vue un échantillon de 10 *Ctenopoma* récoltés à Kassa, à 20 *C. kingsleyae* du bassin de la Volta Noire et à 153 *C. petherici* de la zone d'inondation du Moyen Niger. Les résultats sont indiqués dans le tableau ci-dessous:

| | Nombres d'épines à la dorsale | | | | Moyenne | Variance |
|-----------------------------------|-------------------------------|------|-------|-----|---------|----------|
| | XVI | XVII | XVIII | XIX | | |
| <i>C. kingsleyae</i> , Kassa | | 4 | 6 | | 17,60 | 0,24 |
| <i>C. kingsleyae</i> , Volta | 2 | 18 | | | 16,90 | 0,09 |
| <i>C. petherici</i> , Moyen Niger | | 29 | 121 | 3 | 17,83 | 0,18 |

| | Nombres d'épines à l'anale | | | | Moyenne | Variance |
|-----------------------------------|----------------------------|----|----|--|---------|----------|
| | VIII | IX | X | | | |
| <i>C. kingsleyae</i> , Kassa | | 8 | 2 | | 9,20 | 0,16 |
| <i>C. kingsleyae</i> , Volta | | 18 | 2 | | 9,10 | 0,09 |
| <i>C. petherici</i> , Moyen Niger | 1 | 82 | 70 | | 9,45 | 0,26 |

Les moyennes dorsale et anale des *Ctenopoma* de Kassa diffèrent d'une façon hautement significative de celles des *C. petherici* du Moyen Niger. La forme de la tête et du corps ne concordent pas davantage: il ne s'agit donc pas de la même espèce. Il est vrai que les *Ctenopoma* de Kassa diffèrent aussi des *C. kingsleyae* du bassin de la Volta par le nombre significativement plus élevé d'épines dorsales, mais ils se rapprochent beaucoup des populations de certaines régions de Côte d'Ivoire et du Mont Nimba et sont certainement conspécifiques. Les Poissons du revers oriental du plateau de Bandiagara proviendraient donc finalement du bassin de la Volta, mais leur isolement serait suffisamment ancien pour que les effets de la ségrégation géographique soit décelable chez plusieurs espèces, notamment *C. kingsleyae* et, à un degré moindre, *Gnathonemus senegalensis*. La proportion d'espèces communes avec le Moyen Niger, 8 sur 10, est tout à fait compatible avec cette hypothèse puisque sur les 95 que nous connaissons actuellement du bassin de la Volta Noire, 88 se trouvent aussi dans le Moyen Niger.

En ce qui concerne les Mollusques, nous avons personnellement récolté *Lanistes guinaicus*, *Limnaea natalensis*, *Biomphalaria pfeifferi* *gaudi* et *Gyraulus fouldougouensis* dans le bassin du Niger et dans

celui de la Volta. *Spathopsis rubens* et *Sphaerium courteti* sont largement répandus en Afrique occidentale: nous les avons trouvés dans le bassin du Niger, mais ils n'ont pas été signalés jusqu'à présent dans celui de la Volta dont la faune malacologique nous est d'ailleurs encore mal connue. Les *Spathopsis rubens* de Sanga sont en outre de taille plus réduite, ont une forme plus régulièrement arrondie, une coquille un peu plus allongée et plus comprimée que les *S. rubens* de la zone d'inondation du Moyen Niger. L'*Aspatharia* sp. de Sanga serait une forme voltaïque; il ne peut être rattaché à aucune des espèces du genre que nous connaissons du bassin du Niger, mais nous possédons deux valves provenant de la Bougouri-Ba, un affluent de la Volta Noire et qui n'en diffèrent pas de façon notable. Quant au *Bulinus* sp., il se rapproche de *B. (Physopsis) jousseaumei* que l'on trouve dans le bassin du Niger, mais il en diffère nettement „in the shape of the columella, the open umbilicus, the unusually small copulatory organ and the long mesocone of the lateral teeth of the radula" (MANDAHL BARTH, in litt., 25-II-1960). La faune malacologique de Sanga aurait donc des affinités à la fois nigériennes et voltaïques. Il convient d'ajouter que beaucoup de ces Mollusques peuvent supporter de longs séjours hors de l'eau et que certains vivent normalement en état d'anhydrobiose durant toute la saison sèche. Ils peuvent de ce fait être transportés assez facilement d'un bassin à un autre, ce qui n'est pas le cas des Poissons; aussi ces derniers donnent-ils des indications beaucoup plus sûres au point de vue biogéographique.

IV. ANCIENNETÉ DE CETTE FAUNE

Au Quaternaire l'Afrique occidentale a connu des périodes alternativement plus humides et plus sèches que l'actuelle. Ces variations climatiques ont souvent été accompagnées de modifications importantes dans les réseaux hydrographiques et la répartition de beaucoup d'animaux aquatiques ne saurait être comprise sans elles. Faisant la synthèse de recherches récentes, TRICART (1958) distingue pour le bassin du Moyen Niger les périodes suivantes:

| Période | Climat |
|--------------------|-------------------------------|
| Quaternaire ancien | { phase sèche
phase humide |
| Préouljien | phase sèche maxima |
| Ouljien | phase humide maxima |
| Préflandrien | phase sèche |
| Néolithique | phase humide |

Au Néolithique, dernier épisode humide, le Niger avait son écoulement entravé par les bouchons de dunes préflandriennes qu'il n'avait pas encore déblayés; le seuil de Tosaye était en outre moins creusé par l'érosion différentielle qu'il ne l'est maintenant. Les crues étaient plus fortes et l'inondation s'étendait vraisemblablement au Nord de Tombouctou en direction d'Arawân. Cependant le niveau des lacs aurait été tout au plus supérieur de 2 m à ce qu'il est aujourd'hui en période de plein remplissage. La pluviométrie n'était donc que faiblement excédentaire par rapport aux moyennes actuelles. Il devait y avoir alors un peu plus d'eau que de nos jours dans la vallée du Sourou et dans les rivières drainant le revers oriental du plateau de Bandiagara, mais pas suffisamment pour qu'un réseau hydrographique hiérarchisé s'établisse dans le Séno. Les Poissons de la Volta n'ont donc pas pu venir coloniser la mare de Vendou au Néolithique.

Dans le bassin du Moyen Niger, le Préouljien, l'Ouljien et le Préflandrien ont pu être facilement distingués; on a en effet reconnu l'existence de deux périodes sèches durant lesquelles les nappes alluviales ont été remaniées par le vent. Les dunes qui en sont résultées n'ont pas le même aspect ni la même orientation. Entre temps, à l'Ouljien, le fleuve avait repris son écoulement avec un débit probablement plus élevé que de nos jours. Les rivages ouljien des lacs sont toujours supérieurs de plusieurs mètres aux rivages actuels. C'est également depuis cette époque que le Niger supérieur, ayant débordé le seuil de Tosaye et emprunté la vallée du Tilemsi, s'écoule vers le Golfe de Guinée. Dans le Séno, les mêmes variations climatiques n'ont pas laissé de traces aussi nettes, la Volta Noire supérieure ayant probablement été capturée par la Volta Moyenne et détournée vers le Sud bien avant l'Ouljien. Au sujet du modelé des sables du Séno, S. DAVEAU parle seulement „d'un épisode aride durant lequel aurait régné un climat proprement désertique, puis d'épisodes humides assez courts alternant à plusieurs reprises avec des retours offensifs de la sécheresse". L'ensemble pourrait correspondre au Préouljien (période d'aridité maxima) + Ouljien + Préflandrien. On serait alors conduit à reporter au Quaternaire ancien l'existence dans le Séno d'un réseau hydrographique cohérent. Avant de s'écouler vers le Sud, la Volta Noire supérieure devait se perdre dans une zone d'épandage alluvial et former des lacs dans les parties les plus basses de la dépression du Séno. Le revers oriental du plateau de Bandiagara était normalement drainé vers ces lacs et la faune aquatique pouvait remonter jusqu'à la Falaise. La capture de la Volta Noire supérieure aurait causé la dégénérescence définitive de ce système; durant les périodes sèches ultérieures le vent aurait repris les dépôts sableux, édifiant des dunes avec eux et effaçant complètement les traces de l'ancien réseau hydrographique. Il est évident qu'une faune

aquatique relict e n'aurait pu subsister jusqu'à maintenant qu'en des points où l'eau n'aurait jamais complètement disparu même aux périodes d'aridité maxima; nous supposons qu'il en fut ainsi à Kassa, Sanga et Kani Kombolé.

Il est de fait que certains Poissons peuvent vivre dans des régions désertiques là où une circulation d'eau souterraine maintient un peu d'humidité et d'eau superficielle. Quatre espèces sont connues de l'Adrar mauritanien qui reçoit moins de 100 mm de pluie par an et neuf espèces du Tibesti encore moins arrosé. Les faunes les plus variées se rencontrent dans des collections d'eau permanentes, au fond de gorges rocheuses où coulaient des rivières lorsque le climat était plus humide. Telles sont la guelta de Molomhar dans l'Adrar mauritanien et la guelta de Tottous dans le Tibesti. La vasque de réception de la cascade de Kassa a du constituer au Préoulien et au Préflandrien une guelta permanente comparable à celles que nous venons de citer et où les dix espèces de Poissons que l'on y rencontre encore s'étaient réfugiées. La mare de Vendou, plus récente, aurait été peuplée à partir de cette faune relict e ce qui expliquerait la composition insolite de son peuplement.

Les *Clarias* du groupe *anguillaris-senegalensis*, les *Barbus* du groupe *ablades-deserti* et surtout *B. pobeguini* possèdent une remarquable aptitude à se maintenir dans des stations dont tous les autres Poissons ont été éliminés. Dans l'Adrar mauritanien, cette association spécifique a été signalée dans la guelta inférieure d'Hamdoun; or celle-ci est temporaire et, à certaine période de l'année, complètement asséchée; sa faune ichtyologique est alors détruite. Etudiant la façon dont cette guelta peut être repeuplée DEKEYSER & VILLIERS (1956) font remarquer qu'après les pluies „le ravin dans lequel elle se trouve coule comme un torrent. Les Poissons ne peuvent donc venir que de la partie supérieure du ravin”. Or ces mêmes auteurs n'y ont reconnu „qu'une guelta supérieure, temporaire elle aussi, mais qui est en saison sèche creusée d'un puits. C'est sans doute dans ce puits, peu profond et boueux que se maintient la souche de Poissons susceptible de peupler périodiquement les gueltas temporaires de la partie moyenne du ravin”. A Bamako, nous avons également constaté que *B. pobeguini* apparaît chaque année dans un ruisseau temporaire qui descend de la falaise du point G. Sans en avoir la preuve formelle, nous pensons que ces *Barbus* se réfugient durant la saison sèche dans les eaux souterraines qui existent à l'intérieur du massif gréseux; ils y pénétreraient et en sortiraient par les fissures d'où l'eau sourd en saison des pluies. Le même phénomène pourrait se produire à Sanga et Kani Kombolé. S. DAVEAU estime en effet que le plateau de Bandiagara „possède certainement tout un réseau souterrain de type karstique”, principalement „dans la bande dominant immédiatement la Falaise orientale”.

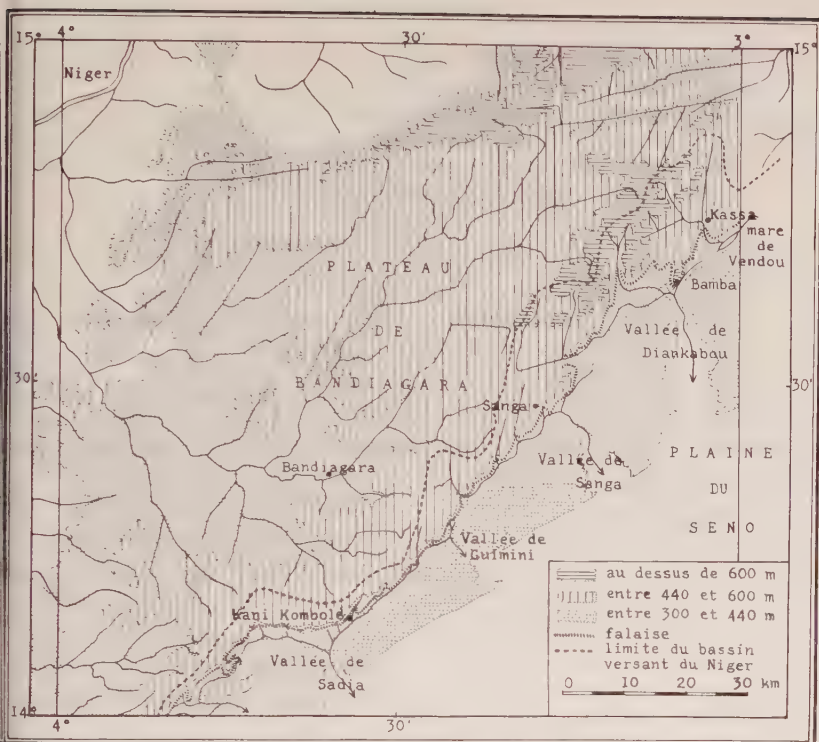


Fig. 1. Hydrographie du plateau de Bandiagara (modifié d'après S. DAVEAU).

RÉSUMÉ

L'existence d'une faune aquatique relictive a été reconnue en trois points différents du revers oriental du plateau de Bandiagara. Cette faune comprend dix espèces de Poissons et huit de Mollusques; les autres groupes zoologiques n'ont pas été étudiés. Elle proviendrait du bassin de la Volta et serait isolée depuis le Quaternaire ancien, époque où la capture de la Volta Noire supérieure par la Volta moyenne aurait provoqué l'assèchement définitif de la dépression du Séno. Au cours des périodes sèches du Préouljien et du Préflandrien, cette faune se serait maintenue dans des conditions comparables à celles existant aujourd'hui dans l'Adrar mauritanien et le Tibesti. Au même titre que les faunes aquatiques de ces régions, celle du revers oriental du plateau de Bandiagara mériterait donc d'être considérée comme une faune désertique.

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Die „Seebälle“ - Ein seltsamer Standort der Blaualgen

von

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(mit 6 Fig.)

Am flachen Schlamm- und Sandufer wie auch am Meeresstrand wurden schon öfters kugelförmige Gebilde beobachtet, welche aus verschiedenen Algen zusammengestellt sind. So werden in der Adria oft Kugeln von *Valonia utricularis* gefunden und HANS GIRG beschrieb sie als var. *aegagropila*. Diesen Namen trug auch eine ganze Sektion der Gattung *Cladophora*. Im Süßwasser sind manche aegagropile Formen bei den Cyanophyceen beschrieben worden (*Scytonema mirabile*, *Tolypothrix lanata*). Es handelt sich immer um rein mechanisch, durch Rollbewegung am flachen Grunde, bedingte Wuchsformen der Algen, die von den festgewachsenen Lagern losgerissen wurden und dann diesen Zustand lebend ertragen können.

Analog den Aegagropilen, welche auch „Seeknödel“ genannt werden, rollen sich manchmal solche kugeligen Gebilde aus abgestorbenen Pflanzenresten zusammen. Diese werden dann „Seebälle“ genannt. Im Meere entstehen sie von Blattresten der *Posidonia oceanica*, welche als walzen- und spindelförmige oder als kugelige Anhäufungen in seichten Buchten hin und her rollen. Im Süßwasser fand MORTON solche Seebälle im Hallstättersee (MORTON 1953) von Lärchennadeln zusammengesetzt, welche die Grösse eines Kindkopfes erreicht haben.

Im Vrana-See (Insel Cres im Quarner-Golf — Jugoslawien) fand ich Seebälle, welche aus Blattresten von den in der Umgebung reich vertretenen *Potamogeton pectinatus* zusammengerollt waren. Sie haben 5—7 cm Durchmesser, sind aus festem Gefüge, und ähneln auffallend denen von *Posidonia oceanica* (Abb. 1a, Beil. 1). So fanden sich im Süßwasser und im Meere Parallelerscheinungen, welche die Folge der Zusammenwirkung der mechanischen Wellenkraft und flachen Unterlage sind.¹⁾

¹⁾ SCHMIDT-RIES verglich sie auch mit den Steppenläufern, welche Steppen vom Winde getrieben werden.

Es ist bemerkenswert, dass so ein Spiel der anorganischen Naturkräfte zu einem Standort des Lebens werden kann, und ganz regelmässig von Organismen und zwar von Blaualgen besiedelt wird. Öffnen wir so eine Kugel, fällt uns ein dünner blaugrüner Streifen auf. Diese von Algen besiedelte Zone bildet eine Schicht, welche sich rings um die Kugel in einer bestimmten Entfernung von der Oberfläche verbreitet (Abb. 1b—Cy). In der Mitte der Kugel, wie an ihrer Oberfläche selbst, sind keine Blaualgen zu finden.



Um diese Begrenztheit der Cyanophyceensiedlung deuten zu können, müssen wir uns ein wenig mit der Betrachtung der ökologischen Verhältnissen an solchen Standorten befassen. — In der Tiefe von 1—2 m, wo unsere Seebälle meistens gefunden wurden, macht sich die Wirkung der Wellen noch sehr bemerkbar. Unter der Wasserturbulenz werden die Kugeln gleichmässig hin und her gerollt und dieses Wälzen übt ständig einen gewissen Druck oder eine Schleifung an ihrer Oberfläche aus. Die so ständig gestörte Oberfläche kann deshalb nicht als Standort einer ständigen Blaualgenvegetation dienen. Diese beginnt sich einige mm tiefer, wo das Licht noch ausreichend ist, zu entwickeln. Das Rollen der Kugel sorgt für die Belichtung von allen Seiten; dadurch werden die Blaualgen immer gleichmässig dem Licht zugewendet, was mit der ebenso allseitigen Entwicklung der Vegetation übereinstimmend ist. — Tiefer in der Kugel wird das Licht zum Begrenzungsfaktor, da seine Intensität nach wenigen mm so abfällt, dass dies selbst für die sonst sehr bescheidenen Cyanophyceen nicht ausreicht. Die Seebälle befinden sich in der Tiefe von 1—2 m, wo im klaren Vrana-See noch cca 80%

des äusserlichen Lichtes vorhanden ist. In das Innere der Kugel, 15 mm unter der Oberfläche, dringt noch sehr wenig Licht durch. Die blaugrüne Zone erstreckt sich im Gebiet von cca 30—0,3 %

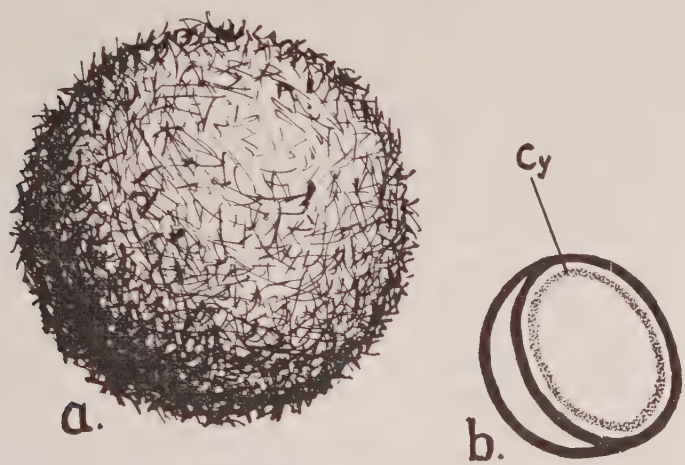


Abb. 1. a) „Seeball“ (natürl. Grösse), b) derselbe, aufgeschnitten; Cy – Blaugalgenzone.

des äusserlichen Lichtes (Abb. 2). — Der Seeboden kommt als Faktor insofern in Betracht, weil er flach und glatt sein muss, um das Rollen der Kugeln zu ermöglichen. Kleine Steinchen und Kalksinterflocken, welche bei der Ballbildung miteingerollt werden, dienen, falls sie in die belichtete Zone geraten, ebenfalls als Ansiedelungskerne der Vegetation. — Es ist leicht annehmbar, dass auch organische Stoffe,

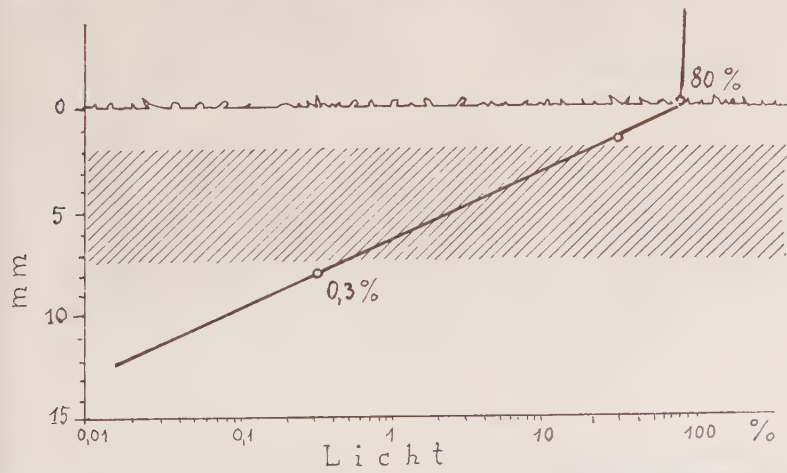


Abb. 2. Lichtabfall im Innern des Seeballes; gestrichelt = Blaugalgenzone.

welche die abgestorbenen Pflanzenreste liefern, das Vorkommen von Blaualgen fördern.

Die Vegetation, welche die belichtete Zone der Seebälle besiedelt, ist hauptsächlich von Blaualgen zusammengestellt. Blaualgen zeigen in mehreren Vertretern eine Neigung zur endophytischen und symbiontischen Lebensweise. So leben einige Anabaenen in der Symbiose mit *Cykas* und *Azolla*. Bei vielen Arten sind die Benennungen „endophytica“ anzutreffen. Eine ganze endophytische Vegetation der roten Cyanophiceen wurde seinerzeit von VOUK im Inneren des Thallus von *Codium Bursa* entdeckt und später auch von FREMY bearbeitet. Die Seebälle sind ein nicht so alter und regelmässiger Standort der Blaualgen wie *Codium*, so hat sich in ihnen keine spezifisch angepasste Vegetation ausgebildet. Sie ist von den bekannten Einwohnern des Littorals zusammengesetzt.

Der beschriebene Standort wird weiter in Mikroverhältnissen gegliedert und von 3 verschiedenen Vegetationseinheiten bewohnt.

1. Den ersten Mikrostandort bieten die Zellen der abgestorbenen Blatt- und Stengelreste von *Potamogeton pectinatus*. Die Blaualgen füllen gleichfalls die Zellen der Epidermis, des Parenchyms und die Tracheen aus (Abb. 3). In den Tracheen kommt eine *Anabaena*-Art vor, welche manchmal die Gefässe auf längere Strecken völlig ausfüllt (Abb. 3/4). Die Verhältnisse sind hier denen der endophytischen und symbiontischen Lebensweise ähnlich, obgleich es sich hier um abgestorbenes Zellmaterial handelt.

In den Zellen des Parenchyms und der Epidermis wurden dünne *Phormidium*-Arten gefunden und zwar *Phormidium angustissimum*

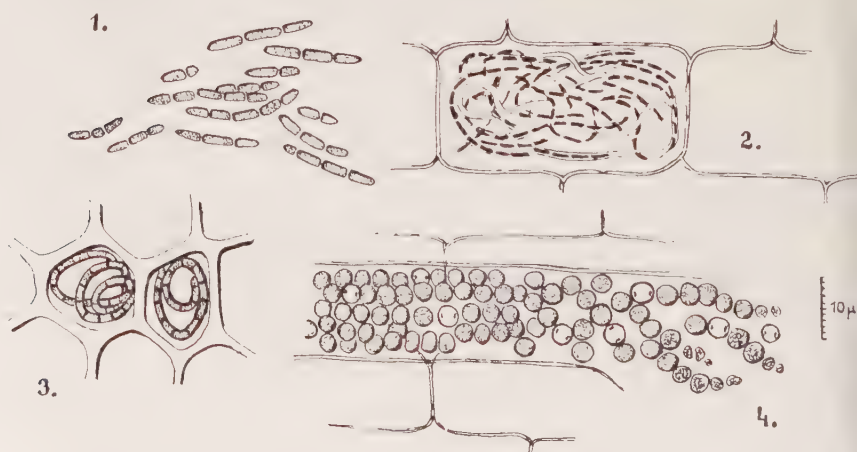


Abb. 3. Vegetation in den Zellen der Blattreste von *Potamogeton pectinatus*: 1. - *Phormidium mucicola*, 2. - *Ph. angustissimum*, 3. - *Ph. mucicola* in den Epidermiszellen eingerollt, 4. - *Anabaena variabilis* in der Blattrachee.

und *P. mucicola*. Das letztere kommt sonst endophytisch im Schleime der Planktonalgen vor. Epiphytisch an den Blättern gedeihen *Calothrix braunii* und *C. parietina*.

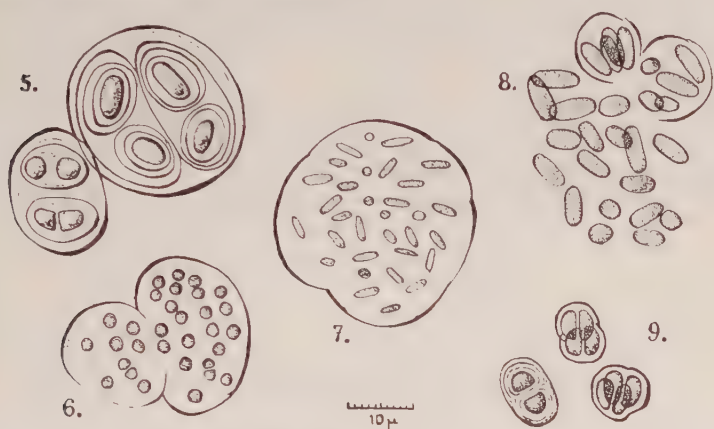


Abb. 4. Vegetation zwischen den Blattresten: 5. - *Gloeotheca palea*, 6. - *Aphanocapsa muscicola*, 7. - *Aphanothece nidulans*, 8. - *Aphanothece microspora*, 9. - *Chroococcus minor*.

2. Eine ganz andere Zusammenstellung zeigen die Verunreinigungen zwischen den Blättern. Hier sind die Chroococcalen vornehmend. Den Arten von *Aphanocapsa*, *Aphanothece*, *Gloeocapsa*, *Gloeotheca*, *Chroococcus* und *Merismopedia* sind stellenweise *Schizothrix delicatissima*, *Tolypothrix distorta* var. *penicillata*, *Oscillatoria sancta* und *O. tenuis*, wie auch die *Calothrix*-Arten beigesellt (Abb. 4).

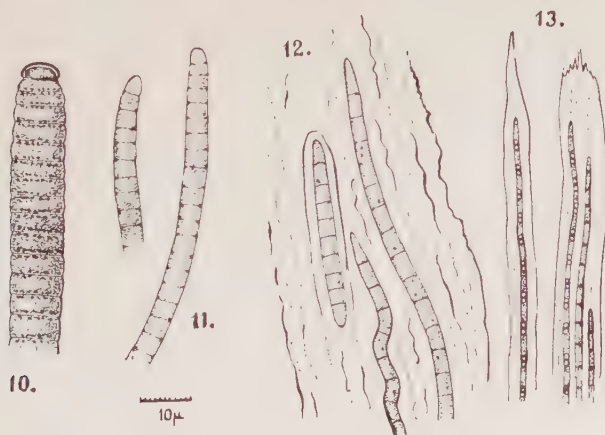


Abb. 5. Vegetation der Kalksinterflocken in den Seebällen: 10. - *Oscillatoria sancta*, 11. - *O. tenuis*, 12. - *Schizothrix arenaria*, 13. - *Sch. lacustris*.

3. Den dritten Mikrostandort stellen die Steinchen und Flocken des Sinters dar, welche in die Kugel miteingerollt wurden (Abb .5). Neben den vorherrschenden *Schizothrix arenaria* und *Sch. lacustri* sind hier in grösseren Mengen *Hydrocoleum homoeotrichum*, *Nostoc verrucosum*, oder *Oscillatoria sancta*, *O. tenuis* und die *Calothrix*-Arten beigemischt.

Die letzte Gruppe unterscheidet sich kaum von der Krustenvegetation in diesen Tiefen, welche aber ausschliesslich am Felsboden anzutreffen ist, wogegen ihr am flachen schlammigen Grund nur in den Seebällen die Lebensmöglichkeiten geboten werden.

FLORA DER CYANOPHYCEEN

1. *Aphanocapsa biformis* A. BR.

GEITLER 1932. S. 158. Fig. 70

Zwischen den Blattresten der Seebälle.

2. *Aphanocapsa muscicola* (MENEGH.) WILLE. (Abb. 4/6)

GEITLER, 1932. S. 160

Zwischen den Blattresten der Seebälle.

3. *Aphanocapsa anodontae* HANSG.

Geitler, 1932. S. 161

Zwischen den Blattresten der Seebälle.

4. *Aphanothece nidulans* P. RICHT. (Abb. 4/7)

GEITLER, 1932. S. 168, Fig. 75c.

W. und G. S. WEST haben eine var. *endophytica* beschrieben welche im Schleime planktonischer Blaualgen wie *Coelosphaerium kützianum* und *Microcystis aeruginosa* gedeihen. Die Alge zeigt also eine Neigung zur endophytischen Lebensweise.

Zwischen den Blattresten der Seebälle.

5. *Aphanothece microspora* (MENEGH.) RABENH. (Abb. 7/8)

GEITLER, 1932. S. 170 Fig. 77

Dimens.: Zellen 3 — 3,5 x 6 — 7 μ ; Zellinhalt glatt, Zellen manchmal leicht gebogen.

Zwischen den Blattresten der Seebälle.

6. *Aphanothece castagnei* (BREB.) RABENH.

GEITLER, 1932. S. 171

Zwischen den Blattresten der Seebälle.

7. *Gloeocapsa* sp.

Dimens.: Zellen 3,5 μ gross, mit eingeschachtelten Hülle

oder zu vielen beisammen. Entspricht der *Gl. atrata*, oder dem farblosen Status von *Gl. kütziana*.

Zwischen den Blattresten der Seebälle.

8. *Gloeotheca palea* (KÜTZ.) RABENH. (Abb. 4/5)

GEITLER, 1932. S. 218

Dimens.: Zellen $3 \times 5 \mu$. Die Hüllen sind ineinandergeschachtelt und, wie SKUJA beschreibt, deutlich geschichtet.

Zwischen den Blattresten der Seebälle.

9. *Chroococcus minutus* (KÜTZ.) NAEG.

GEITLER, 1932. S. 232 Fig. 112

Zwischen den Blattresten der Seebälle.

10. *Chroococcus minor* (KÜTZ.) NAEG. (Abb. 4/9)

GEITLER, 1932. S. 240

Zwischen den Blattresten der Seebälle.

11. *Merismopedia glauca* (EHRB.) NAEG.

GEITLER, 1932. S. 246. Fig. 129

In den Kalksinterflocken im Seebällen.

12. *Calothrix parietina* (NAEG.) THUR.

GEITLER, 1932. S. 604. Fig. 380

Epiphytisch an den Blattresten und in Kalksinterflocken innerhalb von Seebällen.

13. *Calothrix braunii* BORN et FLAH.

GEITLER, 1932. S. 606 Fig. 381

Epiphytisch an den Blattresten und in den Kalksinterflocken innerhalb von Seebällen.

14. *Calothrix* sp.

Dimens.: Fadenbreite 6,8, Zellbreite $2,5 \mu$; gleich lang oder länger als breit. Scheiden fest, braun.

In den Kalksinterflocken im Seebällen.

15. *Tolypothrix distorta* var. *penicillata* (AG.) LEMM.

GEITLER, 1932. S. 719 Fig. 461

Dimens.: Fadenbreite, 10—13 μ ; Zellbreite 7 μ ; Zellen isodiametrisch, in den Meristemen etwas kürzer als breit. Endzelle abgerundet, heller und grösser als die anderen. Scheiden dünn seltener geschichtet, aussen uneben, an den Trichomenden etwas die Trichome überragend und abgeschlossen. Verzweigungen einzeln; die Heterocysten basal.

Zwischen den Blattresten in den Seebällen.

16. *Nostoc verrucosum* VAUCH.

GEITLER, 1932. S. 854 Fig. 542

Dimens.: Zellenbreite 3,5 μ , Heterocysten etwas grösser als die vegetative Zellen. Trichome verflochten. Lager mikroskopisch klein. Scheiden dick, geschwollen, deutlich begrenzt, ähnlich wie sie bei *Nostoc riabuschkini* beschrieben wurde (ELENKIN, 1938. S. 589, Fig. 185).

In Kalksinterflocken in Seebällen.

17. *Anabaena variabilis* KÜTZ. (Abb. 3/4)

GEITLER, 1932. S. 876 Fig. 558

Dimens.: Zellen kugelig, 3,5 μ gross, die Heterocysten von gleicher Grösse, Dauerzellen 5,5—7 μ , tonnenförmig, etwas länger als breit. — Kleiner als der Typus.

Innerhalb der Tracheen der Blattreste im Seebällen.

18. *Oscillatoria sancta* (KÜTZ.) GOM. (Abb. 5/10)

GEITLER, 1932. S. 943 Fig. 598c

Dimens.: Zellbreite, 10,2—12 μ ; Länge 3—4 μ ; an den Querwänden eingeschnürt und granuliert. Endzelle abgerundet, mit Kalyptra, etwas enger als die andere Zellen.

In den Kalksinterflocken und zwischen den Blattresten in den Seebällen.

19. *Oscillatoria tenuis* AG. (Abb. 5/11)

GEITLER, 1932. S. 959 Fig. 611f, g

Dimens.: Zellbreite 4,3—4,6 μ ; Länge 2,5—3 μ . Trichomende kaum verjüngt, manchmal gebogen, an den Querwänden leicht eingeschnürt. Endzelle abgerundet mit leicht verdickter Aussenmembran.

In den Kalksinterflocken im Seebällen.

20 *Phormidium mucicola* HUB.-PESTALOZZI et NAUM. (Abb. 3/1,3)

GEITLER, 1932. S. 997 Fig. 637.

Dimens.: Zellen 1,4—1,6 μ breit, 2—3 x länger als breit. Trichome kurz aus 2—5 Zellen bestehend oder länger, in den Zellen der Blattreste eingerollt. An den Querwänden „getrennt“ und eingeschnürt. Endzelle abgerundet oder leicht konisch.

Diese Art wurde sonst im Schleime planktonischer Algen beobachtet. Es wäre möglich, dass die seltsame Form dieser Alge die Folge der endophytischen Lebensweise ist. Demnach könnte sie als Wuchsform einer anderen oder vielleicht mehrerer *Phormidium*-Arten betrachtet werden.

Innerhalb der Zellen von *Potamogeton*-Blattresten in den Seebällen.

21. *Phormidium angustissimum* W. et G. S. WEST (Abb. 3/2)

GEITLER, 1932. S. 996

Innerhalb der Zellen von *Potamogeton*-Blattresten in den Seebällen.

22. *Schizothrix arenaria* (BERK.) GOM. (Abb. 5/12)

GEITLER, 1932. S. 1085 Fig. 693de

Dimens.: Zellen 2,5—3 μ breit; 2—3 x länger als breit; gegen Trichomenden isodiametrisch. Endzelle leicht verjüngt, abgerundet oder konisch, Scheiden farblos, weit, geschichtet, aussen uneben, einzelne Trichome enthaltend.

In den Kalksinterflocken innerhalb der Seebälle.

23. *Schizothrix delicatissima* W. et G. S. WEST

GEITLER, 1932. S. 1086.

Zwischen den Blattresten in Seebällen.

24. *Schizothrix lacustris* A. BR. (Abb. 5/13)

GEITLER, 1932. S. 1092 Fig. 698, 699

Dimens.: Zellen 1—1,5 μ breit, 2—4 x länger als breit, an den Querwänden eingeschnürt, manchmal mit einem Körnchen an jeder Seite. Endzelle kaum verjüngt, abgerundet. Scheiden weit, aussen uneben, farblos, an den Enden zugespitzt, ein oder mehrere Trichome enthaltend.

In den Kalksinterflocken innerhalb der Seebälle.

25. *Schizothrix affinis* LEMM

GEITLER, 1932. S. 1112

Dimens.: Zellbreite, 1,2 μ ; Länge 1 μ , kürzer als breit. An den älteren Teilen etwas länger. Scheiden dick, geschichtet, braun. In den Kalksinterflocken innerhalb der Seebälle.

26. *Hydrocoleum homoeotrichum* var. *tenue* GOLUBIC

GOLUBIC, 1957. S. 220 und 251 Fig. 5

Dimens.: Zellen 3,4 μ breit; länger, gleich oder etwas kürzer als breit. An den Querwänden nicht eingeschnürt, manchmal granuliert, Trichomende verjüngt. Endzelle kopfig mit Kalyptra. Scheiden farblos, breit, 1 bis mehrere Trichome enthaltend.

In den Kalksinterflocken innerhalb der Seebälle.

Ausser den Cyanophyceen wurden in den Seebällen noch verstreute Diatomeen beobachtet, welche aber in diese Bearbeitung nicht einbezogen sind.

Es wäre empfehlenswert, ähnliche Zönosen in den *Posidonia*

Seebällen zu suchen,¹⁾ sowie auch die Tierwelt dieser seltsamen Biotopen zu untersuchen.

ZUSAMMENFASSUNG

1. Am flachen, schlammigen Ufern des Vrana-Sees fand der Verfasser die sog. Seebälle, welche aus den Blattresten von *Potamogeton pectinatus* zusammengerollt worden sind. Diese Kügelchen stellen eine Parallelscheinung ähnlicher Gebilden im Meer dar, wo sich die Bälle aus den Blattresten von *Posidonia oceanica* bilden.
2. Innerhalb der Bälle, in einer gewissen Entfernung von dessen Oberfläche, wurde eine blaugrüne Zone nachgewiesen, wo eine spezifische Blaualgenvegetation gedeiht.
3. Folgende Faktoren bedingen und begrenzen das Vorkommen dieser Vegetation in den Seebällen: Von aussen wird die Vegetation durch die mechanischen Roll- und Schleifbewegungen etwas tiefer unter der Oberfläche gehalten. Einige mm tiefer wird das Licht zum Begrenzungsfaktor für die Vegetation, so dass sie im Gebiet vom cca 30—0,3% des Gesamtlichtes gedeiht. Das Rollen versichert die allseitige Belichtung, so dass sich die Vegetation gleichmässig um den Ball entwickeln kann. Die Unterlage muss flach sein, um ein regelmässiges Rollen der Seebälle zu ermöglichen.
4. Die Vegetation, welche sich in der belichteten Zone entwickelt, ist hauptsächlich aus Blaualgen zusammengestellt.
5. Der Standort ist weiter in Mikroverhältnisse gegliedert:
 - a) In Zellen und Geweben von abgestorbenen Blattresten kommen folgende Arten vor: *Phormidium mucicola*, *Ph. angustissimum* und *Anabaena variabilis*.
 - b) Zwischen Blättern dominieren die Chroococcaceen, vor allem die *Aphanocapsa*, *Aphanothece*, *Gloeocapsa*, *Gloeothece*, *Chroococcus*, und *Merismopedia* Arten.
 - c) Kalksinterflocken und Steinchen in den Seebällen enthalten: *Schizothrix arenaria*, *Sch. lacustris*, *Hydrocoleum homoeotrichum*, *Oscillatoria sancta*, *O. tenuis*.In allen drei Standorten waren *Calothrix brauni* und *C. parietina* vertreten.

Es wäre empfehlenswert, ähnliche Standorte in den Seebällen aus *Posidoniablattresten* im Meer zu untersuchen, sowie ebenfalls die Tierwelt dieser ungewöhnlichen Biotope.

¹⁾ Meine Befunde der *Posidonia*-Seebälle in Golf Stari Trogir im Mittel-dalmatien zeigten keine Blaualgenvegetation.

SUMMARY

1. On the flat shallow muddy coast of the Vrana-lake (island Cres-Quarner-bay, Yugoslavia) the author found the so called „lake balls” composed from the residuals of *Potamogeton pectinatus* leaves, as an analogous feature to the similar balls found in the sea, composed from death leaves of *Posidonia oceanica*.
 2. Inside such balls a blue green Zone was found in a distinct distance from the ball surface caused by a specific Cyanophycean vegetation.
 3. The factors limiting this vegetation in a slender zone are as follows: From outside the wave-caused mechanical rolling and surface pressure keeps the vegetation something deeper. Some mm deeper in the ball light becomes the limiting factor for the vegetation, so that it extends from about 30—0,3 % of the full outside light. The rolling movement assures the exposure to the light from all sides so that the vegetation can be developed regularly around the ball. The ground has to be flat to enable the rolling movement.
 4. The vegetation developed in the illuminated zone is mostly composed by blue green algae.
 5. The biotop is dealt farther into micro relations,
 - a) In cells and tissues of death leaves of *Potamogeton pectinatus* there are found: *Phormidium mucicola*, *Ph. angustissimum* and *Anabaena variabilis*.
 - b) In the dirt between leaves the *Chroococcaceae* dominate with the species of *Aphanocapsa*, *Aphanothece*, *Gloeocapsa*, *Gloeothece*, *Chroococcus* and *Merismopedia*.
 - c) On the little stone or travertin particles inside of the ball live *Schizothrix arenaria*, *Sch. lacustris*, *Hydrocoleum homoeotrichum*, *Oscillatoria sancta*, *O. tenuis*. This vegetation shows great similarities to the crust vegetation on the rocky shores. On the shallow muddy shores the lake balls are the only biotop where it can survive.
- In all three microbiotops *Calothrix brauni* and *C. parietina* are found.
- It would be of interest to discover similar biotops in the Sea balls composed by *Posidonia* leaves residuals, as well as to look for the animal life in these curious biotops.

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Sur les genres *Keratella*, *Synchaeta*, *Polyarthra* et *Filinia* d'un lac italien

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(avec 2 figs.)

Pour les recherches hydrobiologiques sur le lac de Nemi de UMBERTO D'ANCONA et de ses collaborateurs qui ont été faites à l'occasion de la baisse du lac, recherches dont cet travail fait partie, on renvoie aux travaux des mêmes Auteurs (D'ANCONA 1942); on a repris ici en particulier quelques questions taxonomiques qui ont été suggérées par les résultats des recherches sur les Rotifères du lac de Nemi (PARISE 1960) et complétées par l'observation de formes d'autres localités.

Le lac a baissé de m 21,50 (profondeur originale m 34); une comparaison entre les conditions précédant et suivant la baisse ont permis de constater une modification dans la composition de la faune des Rotifères d'accord avec tout ce que L. VOLTERRA-D'ANCONA (1933) et V. MARCHESONI (1940) avaient remarqué à propos d'autres planctontes.

Cette modification, dans le cas des Rotifères, a consisté surtout en trois faits: 1, l'invasion du centre du lac par des formes littorales (*Brachionus*, *Anuraeopsis*, *Euchlanis*, *Testudinella*); 2, substitution de populations par d'autres affines (*Filinia terminalis* — *Filinia longiseta*, *Asplanchna priodonta* — *Asplanchna girodi*, *Keratella cochlearis* à grande variabilité — *Keratella cochlearis* à petite variabilité, *Polyarthra vulgaris* — *Polyarthra* sp. forme introgressive); 3, disparition du lac de quelques formes (*Kellicottia longispina*, *Conochilus unicornis*, *Keratella quadrata*).

Outre qu'avec la baisse, le premier fait peut surtout être mis en relation avec la modification de la morphométrie des rives, modification qui a déterminé un développement considérable de la végétation côtière: en effet, les formes d'invasion qu'on a remarquées sont en général des formes liées à la végétation. Le second fait, les

formes de substitution, doit vraisemblablement être mis en rapport avec la modification du trophisme du milieu. Quant à la disparition des eaux de quelques formes, troisième fait, il faut remarquer que, du moment que des formes analogues ont été signalées dans les milieux les plus divers, la faible faculté d'adaptation des formes de Nemi amènerait à les considérer comme des populations spécialisées, malgré qu'on ne puisse individualiser aucun détail qui les distingue des formes correspondantes d'autres localités. On a employé ici le terme „populations” parce qu'il n'est pas bien clair en quel sens on peut employer en de tel cas les catégories taxonomiques courantes, telle espèce ou race.

A ce propos, on peut mettre en relief le fait que souvent des populations de Rotifères étroitement semblables, présentent une adaptation écologique assez différente. La possibilité de distinguer des espèces différentes est retenue du fait qu'à l'adaptation différente ne correspond pas une différenciation morphologique suffisante et l'opinion que ces organismes possèdent une forte diffusibilité. Cette opinion est toutefois fondée justement sur le fait que dans de vastes étendues et dans des milieux différents on trouve généralement des formes semblables.

Les quatre genres, qui ont été pris en considération ici parmi les autres du lac de Nemi, ont paru significatifs afin de mettre en relief le fait que, pour certaines espèces acceptées en littérature, le critérium de distinction morphologique n'est pas bien fondé (*Synchaeta tremula* — *kitina* — *oblonga* — *lakowitziana*, *Filinia terminalis* — *maior* et *F. longiseta* — *limnetica*, *Polyarthra vulgaris* — *dolichoptera* — *major*), tandis que d'autre part, si l'on accepte le postulat de la forte diffusibilité, la différenciation écologique particulière permet de retenir que les espèces ou races soient beaucoup plus nombreuses qu'il est possible d'établir par l'observation morphologique. Pour la qualification taxonomique de quelques populations, il serait donc préférable dans ces cas de se confier plutôt qu'à la nomenclature, à la description biométrique et écologique de ces populations, la détermination taxonomique n'étant possible que par des élevages expérimentaux.

Gen. *Keratella*

Keratella cochlearis

Pendant la période 1922—26, on remarque que dans le lac de Nemi alternent deux populations de *Keratella cochlearis* distinctes d'un point de vue biométrique: l'une grande prédominant en hiver et au printemps, l'autre petite prédominant en été et en automne; on trouve les petites formes, bien que peu nombreuses, également en hiver, tandis qu'au cours de l'été avancé les grandes formes dispa-

raissent de l'épilimnion. Il n'est pas clair quels sont les rapports entre cette distribution et les séries de développement de LAUTERBORN; il ne semble pas possible d'établir que l'une dérive de l'autre.

Il est possible que les populations de Nemi constituent deux races distinctes. Quand même on admettrait qu'originellement il se soit agi d'une communauté homogène, l'uniformité relative du milieu lacustre, pauvre en niches, n'a pas déterminé le polymorphisme considérable auquel l'espèce a donné lieu dans d'autres milieux; c'est-à-dire que, du moment que l'on peut facilement supposer de longues périodes de reproduction seulement parthénogénétique, on aurait, en ce cas, seulement deux groupes de clones, l'un à adaptation d'hiver, l'autre à adaptation d'été. L'uniformité biométrique entre ces deux groupes et la différenciation biométrique et écologique de l'un par rapport à l'autre, peuvent faire croire qu'il s'est formé deux races.

Qu'il s'agit de deux races, cela semble confirmé par le comportement de l'espèce pendant la période 1930—42, après la baisse du niveau du lac. Pendant cette période, la grande population disparaît des eaux et les petits exemplaires restent seuls. La disparition de la grande race peut être mise en relation avec la baisse du niveau, parce que pendant la première période elle avait la possibilité d'échapper dans l'hypolimnion aux températures élevées de l'été, tandis que pendant cette seconde période l'hypolimnion ne peut durer tout l'été.

L'hypothèse de PEJLER (1957), selon laquelle les différentes populations de *K. cochlearis* sont distinctes entre elles, semble confirmée. Il n'est pas facile d'établir, toutefois, s'il s'agit de races ou d'espèces.

Keratella quadrata

Cette espèce est présente seulement dans les échantillons de la période 1922—26; après la baisse du niveau du lac de Nemi, pendant la période 1930—43, elle est tout à fait absente.

Les exemplaires des différents échantillons sont tous pareils, soit par rapport à la structure des plaques de la lorica, soit par rapport à l'orientation et aux rapports réciproques des mesures des épines postérieures. Les reliefs délimitant les plaques sont toujours très marqués, les épines postérieures sont parallèles ou, le plus souvent, légèrement convergentes; l'épine droite est un peu plus longue que la gauche, et c'est-là un caractère constant, bien qu'une telle dyssymétrie ne soit en aucun cas remarquable. La longueur totale des exemplaires dans les échantillons les plus abondants varie entre 225 et 300 μ , la longueur de l'épine postérieure droite entre 65 et 100 μ . La variation saisonnière des dimensions est très modeste, elle est comprise dans les mesures sus-dites.

De quatre écotypes proposés par CARLIN (1943), celui auquel la forme de Nemi correspond le mieux, est le groupe *reticulata*. GILLARD (1948) dit que, de ces quatre groupes, deux seuls, *frenzeli* et *quadrata*, peuvent être considérés comme des races écologiques. La forme de Nemi, toutefois, ne correspond à aucune des deux races proposées par GILLARD: ni à *frenzeli*, parce que cette race présente une variation saisonnière considérable et qu'elle atteint des dimensions remarquables dans les épines postérieures; ni à *quadrata*, parce que, sans tenir compte de sa forte variabilité saisonnière et de ses formes souvent asymétriques, c'est une forme d'étang. De même, il faut exclure le groupe *dispersa* à cause de la morphologie particulière de ses épines postérieures et parce que c'est encore une forme d'étang à forte variabilité.

La population de Nemi présente les caractéristiques suivantes: elle est typiquement pélagique et d'une adaptation relativement raide; en effet, elle disparaît tout à fait du lac à la suite de la baisse; elle présente une variabilité très petite de la longueur des épines postérieures en comparaison avec toutes les autres races de *quadrata* qui ont été décrites; on a remarqué un maximum fort considérable au mois d'avril 1925, un autre maximum, moins important, au mois de mai 1926.

Il est donc possible de croire que *K. quadrata* de Nemi est une race écologique particulière, qu'il faut ajouter aux deux races prévues par GILLARD; son identification avec l'écotype *reticulata* de CARLIN peut paraître plus ou moins plausible.

Gen. *Polyarthra*

Tous les exemplaires qu'on a examinés présentent huit noyaux dans le vitellogène.

Dans l'échantillon d'octobre 1922 sont présents quelques exemplaires de *P. major* (long. corps 146—150 μ , appendices long. 128—130 larg. 22—29) et d'autres d'une identification douteuse, qui, à cause de la structure des appendices et du rapport corps/appendices, pourraient être attribués à *P. dolichoptera* (corps 117—120 μ , app. long. 128—130 larg. 11) mais qui ne possèdent pas d'appendices ventraux. Peut-être que ce sont des hybrides *dolichoptera-major*.

Les nombreux exemplaires de juillet 1923 peuvent être considérés comme *P. vulgaris* (corps 80—120 μ , app. long. 73—110 larg. 8—14); quelques-uns d'entre eux présentent toutefois une structure des appendices tout à fait pareille à celle qu'a représentée PEJLER (1956) dans les figures par lesquelles il veut démontrer le phénomène d'introgression entre *P. vulgaris* et *P. dolichoptera*. Il ne paraît cependant pas que des exemplaires typiques de *dolichoptera* soient présents.

L'échantillon de décembre 1932, époque qui correspond au

niveau minimum du lac, présente des caractéristiques particulières. Les exemplaires, très nombreux, présentent un profil frontal nettement rectangulaire, un profil transversal arrondi, longueur du corps 95—120 μ , des appendices 106—128. Ces derniers, toujours plus longs que le corps, sont très minces, 4 μ environ, et frisés dans la partie distale. Les appendices ventraux mesurent en moyenne 50 μ . Les palpes latérales sont situées en correspondance de l'angle inférieur du corps. La structure des appendices latéraux rappelle *P. trigla* EHRB. 1834 et la description par CARLIN de *P. remata* (SKORIKOV) 1856. Le profil frontal concorde toutefois avec *P. dolichoptera* par CARLIN (1943 pl. 2 fig. 1) et PEJLER (1956), mais la section transversale n'est pas aplatie dorso-ventralement, comme le dit NIPKOV (1952). Les appendices ventraux bien développés (ils atteignent jusqu'à 65 μ) et le rapport corps/appendices rappellent *P. longiremis*; selon CARLIN pourtant, le corps de *longiremis* est semblable à celui de *vulgaris* et ses appendices latéraux sont plutôt larges. L'identification de cette population est par conséquent problématique.

Dans l'échantillon d'avril 1934 est présente une nombreuse population, qui par tous ses caractères concorde bien avec *P. dolichoptera*. Les exemplaires sont très grands par rapport aux spécimens des autres échantillons: long. du corps 100—140 μ , des appendices lat. 120—150, ces derniers sont en général bien plus longs que le corps et plutôt minces, 7—12 μ .

Au mois de juillet 1934 les exemplaires sont semblables à ceux de juillet 1923, c'est-à-dire, ils présentent des caractères soit de *vulgaris* soit de *dolichoptera*; corps 87—110 μ , app. lat. 90—110, app. ventr. 40.

L'échantillon d'octobre 1934 est pareil à celui dont on vient de parler: corps 87—124 μ , pap. lat. 87—118. Les appendices sont le plus souvent pennés ainsi qu'en *vulgaris*, mais plutôt minces, 8—14 μ , comme en *dolichoptera*, la forme du corps et la position des palpes latérales sont relativement variables et en faveur tantôt d'une forme, tantôt de l'autre.

Ce n'est qu'au mois d'octobre 1941 que l'on rencontre des exemplaires typiques de *P. vulgaris* par le profil du corps, la forme des appendices lat., le rapport corps/app. lat. et la position des palpes latérales; corps 90—110 μ , app. lat. 90—110, app. ventr. 40—45.

PEJLER dit qu'il a remarqué des formes intermédiaires entre *P. vulgaris* et *P. dolichoptera* (1956) et même entre *P. vulgaris*, *dolichoptera* et *major* (1957). Il est d'avis que ces formes intermédiaires se forment par hybridation introgressive (ANDERSON & HUBRICHT 1938).

D'après les caractéristiques par lesquelles elles ont été décrites, il est pourtant impossible de considérer comme bonnes espèces *P. dissimulans* NIPKOV et *P. longiremis* CARLIN.

CARLIN aussi, en effet, lors qu'il établissait les critères diagnostiques pour les espèces qu'il avait déterminées dans le Motalaström, avait admis que pour ce qui se rapporte à la structure des appendices et au rapport corps/appendices, des exemplaires de *P. vulgaris* peuvent être semblables à des exemplaires de *P. dolichoptera*, et il avait relevé en cette dernière une remarquable variabilité qui, à son avis, conduirait à la distinction de nouvelles espèces.

Même si l'on admet l'hypothèse de l'hybridation naturelle, il est toutefois nécessaire d'admettre que dans le groupe avec huit noyaux dans le vitellogène (*P. vulgaris*, *dolichoptera*, *major*, *longiremis*, *dissimulans*, *proloba*) il existe plus d'une espèce: en effet, l'hypothèse de PEJLER, qu'il s'agit d'introgression, est fondée sur la supposition que les espèces définies par CARLIN sont authentiques. Ce seraient les espèces *P. vulgaris* CARLIN, *P. dolichoptera* (IDELSON) et *P. major* BURCKHARDT; il paraît d'ailleurs que dans la nature des populations typiques de ces espèces n'auraient pas été observées plus fréquemment que les populations hybrides. Cela résulte évidemment des recherches de PEJLER et, indirectement, de celles de CARLIN.

Il paraît que, dans le lac de Nemi, la population prédominante est un hybride *vulgaris-dolichoptera*; tandis que l'hybride de 1932 peut être en rapport avec la baisse.

Par conséquent, il ne semble pas facile d'identifier comme des espèces authentiques tout court, seulement les formes qu'on a décrites comme *P. vulgaris*, *P. dolichoptera* et *P. major*; à son tour peut-être l'hypothèse introgressive n'interprète-t-elle pas d'une façon exhaustive les rapports qui existent entre les différentes formes de *Polyarthra*.

Gen. *Synchaeta*

Les exemplaires de *Synchaeta* de Nemi apparaissent distincts, quant à leurs dimensions, en deux groupes: un groupe aux grandes dimensions, 200—300 μ , et un autre aux petites dimensions, 80—120 μ (exemplaires contractés).

L'oeil est toujours visible et bien évident chez les exemplaires du groupe de petites dimensions, tandis qu'on ne le voit jamais chez les exemplaires de grandes dimensions. Chez les petits exemplaires il ressemble à deux lamelles de couleur rouge foncé, à l'ordinaire égales l'une à l'autre, mais pas rarement de grandeur différente aux contours irrégulièrement ovales; lorsque l'exemplaire est dissous par l'hypochlorite, les lamelles résistent à l'action chimique et on peut les observer isolées de tout le reste, soudées à l'autre. Chez les grands exemplaires, le pigment oculaire ne ressort pas à cause de la longue période de conservation; en effet, dans un prélèvement effectué récemment au lac de Nemi, chez ces exemplaires l'oeil ressort bien

nettement, il est relativement ample (8—10 μ), de couleur rouge clair, en forme de vésicule sphérique. Outre que la distribution, même la nature du pigment oculaire semble donc différente chez les deux groupes.

Le mastax chez les grands exemplaires est du type *pectinata* et chez les petits du type *tremula*. Chez le mastax type *pectinata*, des exemplaires du lac de Nemi (fig. 1, a), les *rami* sont constitués par deux longues lames rectangulaires, dont la surface est tournée vers le plan median, lames qui s'écartent du côté supérieur du

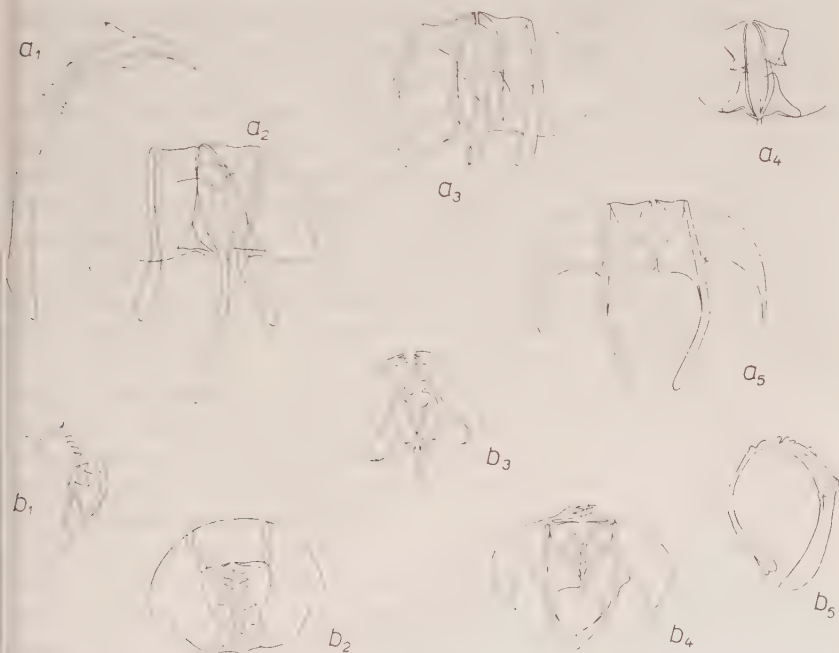


Fig. 1. Gen. *Synchaeta*: a) mastax type *pectinata*: a₁ vue latérale, a₂ v. frontale, a₃ v. polaire inférieure, a₄ v. polaire supérieure, a₅ v. postérieure. b) mastax type *tremula*: b₁ v. sub-latérale, b₂ v. polaire supérieure, b₃ v. frontale, b₄ v. postérieure, b₅ v. latérale.

fulcrum et qui se rejoignent au dos, sans se souder, en délimitant un orifice ovale; le long du premier trait, les deux lames sont un peu plus larges et, en direction du bord supérieur, elles s'inclinent vers l'extérieur en forme d'entonnoir. Le long du bord inférieur de chaque lame est insérée latéralement une petite feuille en forme de voile, arrondie au bord libre. Depuis la moitié environ jusqu'à la termination dorsale, sont soudées latéralement aux *rami* deux lamelles triangulaires, les *unci*, dont chacun est joint, vers l'angle extérieur et libre, au *manubrium*. Le *manubrium* est un

petit bâton aplati et, peu après la moitié de son cours, plié an avant; il porte deux feuillets, dont l'un est petit, triangulaire, émoussé à l'angle libre, tourné vers le plan median jusqu'à toucher à peu près son contre-latéral, et dont l'autre, en forme d'ample voile, est tourné latéralement et en avant, et soudé au tiers supérieur du *m a n u b r i u m*; dans la partie inférieure de cette soudure on voit sur le *m a n u b r i u m* une petite apophyse triangulaire, aigüe, qui quelquefois peut être aussi bifide. Bien plus difficile à observer est la structure que l'on rencontre près de l'orifice délimité par les *r a m i*: dans la partie ventrale de cet orifice on voit une lame trapézoïdale qui, pliée en forme de douche le long de la ligne médiane, saillit de l'orifice, elle se courbe latéralement sous (ou sur) les *r a m i* et saillit à côté de ceux-ci en forme de deux lamelles triangulaires qui adhèrent aux petites feuilles latérales des *r a m i* nommés ci-dessus; le côté inférieur de ces deux lamelles est sinueux et ne coïncide exactement pas avec le bord inférieur des petites feuilles. Il y a tout près de la partie plus dorsale des *r a m i* une autre lame qui commence au niveau du côté postérieur des *u n c i* et qui se pousse en avant, pliée en forme de douche (ou coupée par une incision) le long de la ligne médiane. L'ensemble de l'appareil semble fonctionner en relation au pressage et sucement de la proie.

Chez le mastax type *tremula* (fig. 1,b), au contraire, les *r a m i* sont formés chacun par une courte lame aux bords très épais; suivant une perspective ventrale on voit, d'une façon bien distincte, que les deux bords, en premier lieu le bord l'inférieur et ensuite le bord supérieur, s'écartent du *f u l c r u m* en délimitant un petit orifice qui reste en partie occlu, même en ce cas, par une lame trapézoïdale à douche qui, le long de la ligne médiane, saillit de l'orifice et saillit latéralement à côté des *r a m i* et vers la partie inférieure. La partie de cette lame qui se présente latéralement en dehors de chaque *r a m u s*, est en forme de lobe et adhère au feuillet, étendu en forme de voile, qui est soudé latéralement aux *r a m i*. Les bords supérieurs des *r a m i*, après un bref cours arqué, se rejoignent postérieurement aux bords inférieurs (toutefois ce détail n'est pas bien clair), ces derniers bords se soudent latéralement aux *u n c i*, au niveau du troisième denticule (considérant comme le premier, en ce cas et après, le denticule plus ventral) en se ramifiant — il semble — en deux terminaisons dont la première, tournée vers la région ventrale, passe sous le premier denticule, et la seconde sous le troisième. Les *u n c i*, dont on a déjà vu leur insertion avec les *r a m i*, consistent en deux robustes lames dentelées; dans chacune de ces lames les trois premiers denticules se présentent comme des lamelles bien pointues, le premier denticule a sa pointe tournée ventralement, le troisième vers le plan médian, et enfin le second reste en position intermédiaire.

Le troisième denticule est séparé du quatrième par une incision plus ou moins profonde, sa présence est vraisemblablement en rapport au fait que les trois premiers denticules sont insérés sur la terminaison du *ramus*, tandis que la série successive est soutenue par le *manubrium*. Chez quelques exemplaires cette incision est relativement ample, égale au moins à la largeur d'un de ses denticules limitrophes, mais il s'agit toutefois d'un caractère assez variable. En effet, dans quelques mastax elle se réduit à une fente étroite qui, étant plus définie et surtout plus profonde, se distingue toujours de toutes les autres; chez le même mastax, ces fentes présentent toujours une ampleur différente dans l'une et dans l'autre des lames unciales, et de plus, elles ne se trouvent pas au même niveau, car naturellement d'un côté il correspond à chaque incision la pointe d'un denticule de l'autre. A cette fente succède une seconde série de trois ou quatre denticules. En général, les denticules de cette série sont au nombre de quatre, mais il m'est arrivé quelquefois, malgré une observation soigneuse, d'en voir seulement trois sur une lame, et régulièrement quatre sur l'autre; il faut observer, à ce propos, qu'il est parfois difficile d'interpréter le dernier denticule, parce qu'il semble être formé par la fusion de deux denticules. Pourtant, dans l'ensemble les denticules sont généralement au nombre de sept, et quelquefois on en voit seulement six. Au delà du dernier denticule il y a une autre incision profonde bien plus large que la précédente et suivant la dent par laquelle se termine l'uncus; la dent prend son origine de l'épaississement latéral de la lame de l'uncus; elle est longue, sinueuse et pointue; près de sa racine l'uncus se joint au manubrium. Même en ce cas, le manubrium est un petit bâton auquel sont soudées deux lames subtiles: une lame médiane en forme triangulaire qui présente une très large insertion, mais qui se subtilise rapidement dans une pointe assez émoussée, et une autre lame latérale qui est bien plus ample, en forme de coupole, dont le bord inférieur s'éloigne du manubrium par un petit épaississement triangulaire, passe latéralement et en avant jusqu'à rejoindre le feuillet latéral du *ramus* correspondant.

Les deux types de mastax, qu'on vient de décrire, pourraient correspondre à ceux qui ont été attribués par ROUSSELET (1902) aux espèces *S. pectinata* et *S. tremula*; cela n'est cependant pas tout à fait certifiable.

Le mastax type *pectinata*, qu'on a décrit, présente, à l'égard de celui de ROUSSELET, quelques différences: les lames du manubrium sont plus amples et d'insertion différente, les uncus sont disposés d'une autre façon, le fulcrum est plus large et n'est pas plié dans le trait terminal, et en plus il possède une lame médiane en forme de douche qui n'apparaît pas dans le dessin de ROUSSELET. Les

différences sont remarquables, mais il peut apparaître qu'elles soient dues à des difficultés d'observation. On ne peut dire par conséquent qu'il s'agit certainement d'un mastax différent. D'ailleurs, dans la monographie de ROUSSELET on ne fait pas mention d'éventuelles différences de détail à propos de mastax type *pectinata* en d'autres espèces lacustres (en effet, on ne dit même pas s'il y a d'autres espèces de ce type de mastax), et même la littérature postérieure n'offre aucun élément à ce propos.

J'ai trouvé un mastax égal à celui que j'ai décrit chez des exemplaires du lac de Garda. Les espèces lacustres auxquelles on pourrait l'attribuer, outre que *S. pectinata*, seraient *S. stylata*, *S. grandis* et *S. longipes*; de celles-ci, en effet, ROUSSELET ne décrit pas le mastax. Selon VOIGT (1957) *S. grandis* et *S. longipes* possèdent une dent dans les *unc*i, mais on ne sait pas comment elle est disposée. Si l'on prend même en considération cette observation, il ne reste que deux espèces, *S. pectinata* et *S. stylata*, auxquelles on pourrait attribuer ce type de mastax.

Même le mastax type *tremula*, dont on a parlé ci-dessus, présente des différences remarquables à l'égard de l'homonyme de ROUSSELET: les *ram*i se soudent à l'*unc*us d'une façon tout à fait différente (on fait allusion ici au mastax de *S. oblonga* de la fig. 10, qui, selon ROUSSELET est „very much like” à celui de *S. tremula*), les lames du *manubrium* ont une structure différente, une lame en forme de douche se trouve au milieu des *ram*i et en particulier (on considère ici la fig. 3b, de ROUSSELET) la lame de l'*unc*us ne présente pas avant l'incision deux denticules et un lobe tourné en sens ventral mais trois denticules d'étendue égale, et après l'incision les denticules sont régulièrement quatre et non pas trois. Toutefois même dans ce cas on ne peut dire qu'il ne s'agisse pas du même mastax. On peut réduire les différences seulement au nombre des denticules, qui sont sept au lieu d'être cinq; d'après le dessin susdit je pense donc que le premier denticule n'a pas été représenté d'une manière correcte et que la structure du dernier n'est pas très claire, ce qui a été remarqué ci-dessus.

Le mastax type *tremula* a été attribué à quatre espèces: *S. tremula*, *S. oblonga*, *S. kitina*, *S. lakowitziana*. WESENBERG-LUND (1930) pense que *kitina* et *tremula* sont la même espèce. De *kitina* on ne possède aucun dessin de mastax.

Pour ce qui concerne les dessin de mastax en littérature, les *unc*i de *lakowitziana* (LUCKS 1930, HAUER 1952) seraient bien différents des *unc*i de *tremula* (ROUSSELET 1902). Ce n'est pas de l'avis de CARLIN (1943) qui, au contraire, attribue à *lakowitziana* des exemplaires de *Synchaeta* du Motala dont les *unc*i correspondent sans doute, suivant sa description, à ceux de *tremula* (dénomination qui, selon

CARLIN, est synonyme de *truncata* HOFSTEN). Cet auteur enfin affirme que *truncata* correspond à *lakowitziana*, dont la dénomination est à préférer aux autres, parce qu'elle a une description meilleure.

Réserve faite de la question de synonymie soulevée par CARLIN, je pense que les dessins de la lame unciale de LUCKS et de HAUER sont inadmissibles et qu'il faudrait confronter aussi la lame de *oblonga* décrite par ROUSSELET, car cet examen pourrait représenter, dans l'affirmative, un bon élément de distinction entre ce groupe de formes. Faute de cela, on ne peut pas affirmer que les quatre espèces: *tremula* MÜLLER (ou *truncata* HOFSTEN), *oblonga* EHRB., *kitina* ROUSS., *lakowitziana* LUCKS, puissent être identifiées selon la structure du mastax. On ne veut toutefois conclure que les quatre espèces soient inadmissibles, même si la distinction entre l'une et l'autre a été mise en doute par des auteurs bien expérimentés, tels que: WESENBERG-LUND (*tremula-kitina*), CARLIN (*tremula-lakowitziana*), PEJLER (*tremula-oblonga*).

On a déjà remarqué qu'il y a à Nemi deux populations nettement distinctes l'une de l'autre par leur dimensions. Cette condition semble être relativement commune à beaucoup d'endroits, tels que la lagune de Venise, le lac de Garda, le Motalaström (CARLIN), les lacs danois (WESENBERG-LUND), les lacs de la Suisse (WEBER & MONTET); quant aux grandes formes, on se rapporte généralement à *S. pectinata*, quant aux petites formes on s'adresse à l'une ou à l'autre des espèces du groupe *tremula*. Dans la lagune vénitienne il y a naturellement des formes tout à fait différentes de celles dont on a parlé ci-dessus; dans le lac de Garda les grandes formes sont en rapport avec *pectinata*, tandis que les petites ne correspondent pas — cas remarquable — au groupe *tremula*. Dans le lac de Nemi les populations correspondent normalement à *pectinata* et au groupe *tremula*.

Gen. *Filinia*

La description de *F. longiseta* EHRB. peut être acceptable même pour des populations différentes l'une de l'autre; j'en ai pu observer deux: l'une du lac de Nemi et l'autre d'un étang près de Padue; toutes les deux présentent la soie postérieure (généralement pliée en avant et en haut chez les exemplaires conservés) articulée, et insérée sur la région ventrale sans une dilatation particulière à la racine et dans la troisième partie inférieure du corps. Ces deux formes se distinguent spécialement par deux caractéristiques: la forme d'étang présente les soies recouvertes de spicules bien développées, tandis que chez celle du lac les spicules sont à peine visibles et ressemblent à de petits noeuds disposés le long de la soie; le rapport entre soie postérieure et soies latérales est différent, car chez les formes d'étang la soie postérieure est proportionnellement un peu

plus longue; pour ce qui concerne la distance entre l'insertion de la soie postérieure et le bout postérieur du corps, il s'agit d'un caractère variable selon l'âge de l'organisme et le stade d'ovulation, surtout chez la population d'étang, par conséquent, ce caractère n'est pratiquement pas utilisable. La forme d'étang s'accorde mieux que celle du lac avec *longiseta* EHRB.; la forme du lac ne s'accorde pas avec *limnetica* ZACHARIAS.

Outre ces deux formes, il y en a d'autres, en littérature, telles que *limnetica* ZACH., forme de grande profondeur et dont le rapport soie post./soies lat. est différent des autres qu'on a mentionnées; selon VOIGT (1904) cette population se trouve pendant l'été au niveau supérieur, tandis qu'il y a une autre forme de *longiseta* qui vit en hiver au niveau supérieur et en été en grande profondeur; en outre, il faut citer les formes de *longiseta* observées par SKORIKOV (1896) et par TARNOGRADSKY (1925), qui dans l'ensemble présentent des mesures plus petites que celles des populations précédentes.

La description de *F. terminalis* PLATE peut aussi se rapporter à plusieurs populations. J'en ai observées trois, dont deux du lac de Nemi et l'autre du lac de Garda. La première forme se trouve dans plusieurs échantillons du lac de Nemi pendant la période qui précède la baisse des eaux, elle se présente toutes les années entre 1922 et 1926: longueur du corps 100—150 μ , soies latérales 335—435 μ , soie postérieure 267—350 μ ; les soies sont recouvertes de spicules très minces et clairsemées, la soie postérieure est insérée par une large dilatation tout près du bout postérieur du corps et elle est toujours tournée en bas. La deuxième forme se trouve seulement au mois d'avril 1934 (pendant la baisse du lac de Nemi): longueur du corps 180—230 μ , soies latérales 390—540 μ , soie postérieure 260—360 μ ; soies recouvertes de spicules clairsemées mais grosses, soie postérieure insérée par une large expansion à côté du bout postérieur et toujours tournée en bas; il y a une analogie considérable entre cette forme et la forme précédente pour ce qui concerne l'insertion de la soie postérieure; la différence la plus remarquable consiste dans les dimensions et le rapport soies lat./soie post.; il faut remarquer toutefois que cette dernière population est formée uniquement (d'après les très nombreux exemplaires qu'on a observés) par des femelles mictiques, avec leur caractéristique oeuf durable. Peut-être qu'il s'agit de la même population mais en des conditions biologiques différentes. La troisième forme, celle du lac de Garda, est une population hivernale qui vit en profondeur: longueur du corps 100—150 μ , soies latérales 440—460 μ , soie postérieure 360—375 μ ; forme du corps, spicules et insertion des soies comme chez la première forme.

A ces formes il faut ajouter la population hivernale du Motala-

ström examinée par CARLIN (et attribuée à *maior* COLDITZ, que CARLIN considère comme une espèce bien distincte de *F. terminalis* PLATE), les populations de la Suède observées par PEJLER, etc.

Quant à la taxonomie du groupe „*terminalis-maior-longiseta-limnetica*”, je pense, d'accord avec PEJLER, et non pas avec CARLIN et VOIGT, que le nom de *F. terminalis* PLATE est propre aux formes européennes de *Filinia* qui ont une soie près du bout inférieur du corps (d'ailleurs, on ne sait pas comment il est possible d'admettre — selon l'opinion de VOIGT (1957) — que des formes indiennes, et non pas européennes, correspondent à une espèce que PLATE avait établie pour une population européenne; il serait plus logique de ne pas admettre cette dénomination). Au contraire, c'est une question tout à fait différente que d'affirmer que les populations correspondant soit à la description de PLATE soit à la description de EHRENBORG appartiennent toutes à la même espèce, comme on peut voir à propos des populations rapportées ci-dessus. Cependant, il n'est pas possible de distinguer des espèces dans ce groupe seulement du point de vue biométrique.

CARLIN même remarque que beaucoup de formes sont liées l'une à l'autre, par les rapports de mesures, en variation continue, et PEJLER démontre pratiquement cette liaison en réunissant en diagramme toutes les mesures européennes de *Filinia* du groupe susdit qu'il a pu rencontrer; ces mesures se partagent en deux essais de points, déterminant ainsi les deux groupes „*terminalis* et *longiseta*”. Toutefois, ce diagramme bien qu'il soit en faveur des considérations qu'on a rapportées ici, ne me semble pas tout à fait persuasif; il est

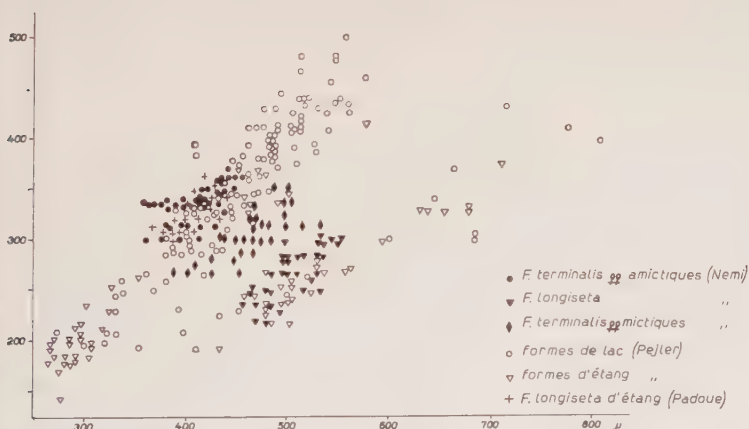


Fig. 2. Gen. *Filinia*, longueur des soies latérales (abscisse) et de la soie postérieure (ordonnée) des exemplaires du lac de Nemi (plein noir), des exemplaires reportés de PEJLER 1957 (à seul contour), des exemplaires d'étang près de Padoue (+).

représenté par la figure 2, où l'on peut remarquer que la *longiseta* d'étang (Padoue) se superpose aux *terminalis* européennes et, tandis que la *terminalis* et la *longiseta* du lac de Nemi s'accordent parfaitement avec les correspondantes européennes, la population de *terminalis* mictiques de Nemi se dispose à joindre les deux essaims de points. Le critérium biométrique ne peut donc toujours servir.

Le seul critérium pour distinguer les deux groupes de populations je pense, est celui qui, tirant son origine de PLATE, regarde l'articulabilité de la soie postérieure, qu'on a adoptée ci-dessus. Chez le gen. *Filinia* on peut distinguer par conséquent, parmi les autres, deux groupes sous la signification, peut-être, de super-espèces. C'est-à-dire le groupe *longiseta* à la soie postérieure articulée et insérée ventralement plus ou moins loin du bout postérieur du corps et plus ou moins développée par rapport aux soies latérales; et le groupe *terminalis* à la soie postérieure qui n'est pas articulée, mais insérée à côté du bout postérieur du corps par une large expansion et, en proportion des soies latérales, relativement plus longue que celles du groupe précédent.

On peut distinguer entre ces deux groupes un très grand nombre de populations sous la signification d'espèces ou de races, dont la détermination exacte, plus qu'à la morphologie, est relatée aux conditions écologiques. Il est probable, en effet, que les formes de *longiseta* du lac de Nemi et des étangs près de Padoue, appartiennent à des espèces différentes, car il est possible de faire quelque distinction morphologique; toutefois il est probable qu'également les *terminalis* de différents milieux, comme les formes de Nemi et du Garda sus citées, appartiennent à des espèces différentes, même si l'on ne peut pas faire cette distinction.

RÉSUMÉ

On a considéré ici quelques formes des genres *Keratella*, *Polyarthra*, *Synchaeta* et *Filinia*. On a relevé, dans le lac de Nemi, deux races écologiques chez *Keratella cochlearis*, et une écologique chez *K. quadrata*. Chez le gen. *Polyarthra* on a observé que l'on trouve, suivant l'hypothèse de l'introggression par PEJLER (1956), bien plus fréquemment des formes hybrides que des formes typiques. Chez le gen. *Synchaeta* on a décrit en détail les mastax type *tremula* et type *pectinata*; on a exprimé l'opinion qu'il n'est pas possible de distinguer entre elles, par la structure du mastax, les formes *S. tremula* (ou *truncata*), *S. kitina*, *S. oblonga* et *S. lakowitziana*. Chez le gen. *Filinia* on pense qu'il soit possible de distinguer morphologiquement *F. longiseta* et *F. terminalis*, mais il est possible qu'à ces deux formes correspondent plusieurs espèces.

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Experiments in Reversion of the Filling up Processes in Fish Ponds

by

S. EHRLICH

(With 13 figs.)

MECHANISM OF FILLING UP

The point of view which regarded the eutrophy of a lake as a process leading to filling up has been recently revised. However, even WUNDSCH (1958) opposing the theory of rapid filling up of an eutrophic lake presumes an "explosion" of filling up after external causes made the lake shallow enough to permit the development of bottom rooted (especially the emergent) vegetation. The same factor or insufficiently rapid deterioration may account for the filling up of the artificial ponds: „Ainsi qu'il a été dit pour les lacs, on appellera eutrophe un étang où il y a une forte productivité primaire et une faible minéralisation: l'ensemble de la biomasse produite dans l'année n'est pas totalement minéralisée par les Bactéries et transformée en matières minérales; il y a donc accumulation de vase organique." (WURTZ, 1958, p. 383).

A question may be raised regarding the reasons for the insufficiently rapid deterioration rate as reducers and consumers are generally known to adjust their numbers and activity to the amount of food provided. In sewage treatment and other artificial situations much larger concentrations of organic matter are broken down than in a fish pond. Fish ponds are also able to "digest" vast quantities of organic matter furnished by inundated green manure cultures. WURTZ (1960, p. 9) quotes a case of sufficiently rapid and complete turnover in ponds having a bountiful algal production.

These facts make it reasonable to assume that a specific inhibition of the breaking down processes is responsible for the accumulation of emergent remnants in ponds, rather than the excessive level of the primary production. THIENEMANN (1925, p. 194) thinks the lack of animal feeding on green, living water plants to be the cause of the

existing type of water body balance. GAJEVSKAJA (1958, p. 354) found that even deep emergent vegetation cannot be attacked by the aquatic invertebrates unless previously shredded artificially, as the thick outer integuments prevent their feeding. Owing to the resistance of the emergent plant tissue to the attacks of the aquatic invertebrates, the importance of these invertebrates in the weed disintegration is negligible. They play a secondary role, feeding on microorganisms, as it was found by SMIRNOV (1958) in the bogs. However, even the microorganisms are unable to complete the decomposition of the emergent vegetation remnants. YOFFE (1954) found the cut coarse weeds to be extremely resistant to decay in comparison with other plant materials. The rotting of underground parts of these plants may also be slowed down by the protection of a network of living roots, which according to BERESOVA & REMPE (1953) excrete substances inhibiting the development of cellulose bacteria.

As the rough weeds increase in extent and the dead vegetation layer on the bottom builds up, the nutrient supply from the open water and bottom is cut off. Suitable conditions for succession leading to sedge development, followed by green mosses and eventually *Sphagnum* come into being. This bog community creeping on the banks impedes nutrient drainage from the adjacent land, lowers the pH of draining water and in many ways intensifies the rate of filling up of the water basin. Unchecked development of the emergent vegetation seems to be the starting point of the ageing processes. Thus, nutria (*Myocastor coypus* MOLINA) was introduced, as a plant feeding water mammal, able to live in dense populations depleting the water vegetation.

THE INFLUENCE OF NUTRIA ON THE FILLING UP PROCESSES IN THE FISH PONDS

The experiments at Podgorzyn, Poland

The site

The Fish pond farm Podgorzyn, where carp and trout are raised is located in the South-West of Poland, near Jelenia Gora, at the foot of the Sudety Mountains, approximately 500 meters above sea level. The ponds are supplied with the water by the mountain stream Czerwona Woda. The ponds are yearly drained and kept dry during the winter. The development of the ponds during the last 30—40 years can be followed from the farm records and information supplied by the pond manager; and during the years 1948 to 1956 by the direct observations by the author.

Approximately 20 years before the start of the experiments, the shallower parts of the ponds emerged so far that according to the farm reports hay making was started on the meagre meadow that took place of the water surface. The encroachment of the ponds progressed in spite of the cutting down of emergent vegetation, the pulling out the sedge tussocks and the other control measures tried. The overgrowth was mainly reeds (*Phragmites communis*), cattails (*Typha angustata*) and bulrushes (*Scirpus* sp.). In the shallower section of the ponds these plants were crowded out by sedges (*Carex* sp. sp.). In the border zone between high weeds and sedges some horsetail (*Equisetum* sp.) could also be found. The domination of sedges over the high weeds was observed as a gradual increase of sedge beds and confirmed by finding living rhizomes of cattails, reeds and horsetail under the sedge tussocks. The lower sections of the sedge fen had typical *Magnocaricetum* appearance: big, densely spaced, but clearly set apart tussocks crowned by luxuriant leaf tufts.

Gradually the *Magnocaricetum* community passed into more or less flat areas of *Parvocaricetum* with green moss and *Sphagnum* development.

For the experiment two ponds, where choking emergent growth and bog encroachment were most pronounced, were chosen. These were the Duzy Lisi pond and Lesny pond. In the Duzy Lisi pond at the start of the experiment the area below water level was mostly overgrown by bulrushes and reeds and bordered by *Magnocaricetum*. Minute brooks which seeped into it among the sedge tussocks were occasionally fringed by *Menyanthes trifoliata*, indicating (according to RALSKI, 1946, p. 118) the comparatively high fertility and flow of the bog water. In the upper parts of the bog *Magnocaricetum* gave way to *Parvocaricetum*. In its hollows green mosses developed and *Sphagnum* cushions covered the crests of the small, stunted tussocks. The bog vegetation crept up on the lower sections of the surrounding meadow.

In Lesny pond, the high emergent weeds consisted of reeds and cattails with occasional isolated isles of bulrushes. Up the swamp the high weeds were crowded in by tremendous sedge tussocks which closed gradually, forming a lush community of *Magnocaricetum*. In its uppermost section the fen changed into an almost flat, well developed *Parvocaricetum* region with a slight green moss development and no *Sphagnum* at all. The more eutrophic character of this pond in comparison with Duzy Lisi pond may be the consequence of a better water supply. Lesny pond has a steady water flow, getting its water directly from the stream and supplying further ponds. This is unlike the Duzy Lisi pond, which obtains water from ponds above and has no outlet flow.

Nutria influence on the Lesny pond

Lesny pond which is 8 hectares in area was fenced in and stocked with 60 male and 500 female subadult nutria in the autumn of 1951. Reproduction began in spring, 1952. Emergent plant growth was depleted during the spring, and in the early summer of 1952 small patches of interlaced roots and rhizomes were seen floating, indicating intensive root cutting by nutria. The area thus cleared of emergent weeds was initially overgrown by *Callitriche* sp., which were eventually shaded out by a heavy growth of duckweeds (*Lemna* sp.).

Nutria settled in the branch heaps provided by the breeders and on the big tussocks along the fen edge. Up the fen, and away from water they grazed only. Continuous grazing of leaves, sprouts and buds finally cut down the tussocks below the water level. Rapid decay of the immersed parts of the beheaded tussocks commenced as suggested by the water turbidity and constant subsidence of the fen. A further indication of decay as well as a factor producing further *Caricetum* deterioration, was mass feeding of carp in the area of the inundated fen (CAHN, 1929). The passing of the boat along the fen edge drove away dense shoals of fish, whereas in other ponds the carp avoided the sedges. The carp laboriously worked their way among the tussocks, creating trails distinguishable from nutria runs. As a result of carp feeding the fen was dotted with deep funnels reaching down to the mineral bottom.

After the regular draining of the pond in the late autumn of 1952 an entirely different picture appeared in comparison with the previous years. The flat areas of *Parvocaricetum* had disappeared. Instead the entire area was covered with dead, well separated big tussocks only. This may indicate that during the development of the fen, as trophism decreased and the growth of the big sedges waned, the small forms filled hollows among the big tussocks and crept over their tops, creating a flat sod. The pulling apart of this sod by nutria, followed by its disintegration revealed the dead, big tussocks, which owing to their lack of food value were ignored by nutria and resisted decay longer. The hollows among the tussocks partly showed mineral bottom. The whole picture was of a dead *Magnocaricetum*.

The channels cut into the fen in 1952 permitted the nutria to swim and dive freely among the remaining dead tussocks, whereby the entire fen area became available for nesting. In 1953, nutria covered the slightly immersed tussocks with litter and settled on them. Tussock depletion continued during 1953 and 1954, until the fen area could be traversed by boat. Scattered tussock remains still

present after the 1954 draining were soft and slimy, showing advanced deterioration. The recesses among the deteriorating tussocks were covered with black, thin muck-ooze probably resulting from the sedge decomposition. Some tussocks were slightly covered by sand, indicating transport of mineral silt on the rotting fen as one of the possible factors stimulating its decay.

During this period the mineral bottom had been almost entirely denuded throughout the former reed and cattail area. The only vegetation remnants there were scattered stubbles of emergent weeds moved in the former years. The stubbles stood slack in the soft mud. Pulling them revealed no roots. Probably these dead stubbles lost their link with the living roots and did not float up together with them. The thick, living mat of roots and rhizomes, which formerly could bear the weight of a man, disappeared entirely, revealing soft, black muck in the hollows and sticky, mineral bottom in more exposed places. Shredded vegetation debris were carried by the wind into one corner of the pond.

Nutria influence on the Duzy Lisi pond

Duzy Lisi pond was stocked with approximately 1,250 nutria from the Lesny stock in late autumn 1952. The fenced area of approximately 10 hectares included 2.5 hectares of water, mostly overgrown by bulrushes, 2 hectares of bog and swamp and the rest of the area was ditches, mineral meadow and a rocky hill overgrown with bush, oaks and pines.

Because of the extensive nutria stock the emergent vegetation was immediately destroyed after the pond had been filled in spring, 1953. No floating vegetation mats could be seen. During the 1953 breeding season shelters were furnished by the breeders, who brought in extensive amounts of branches, cattails, sedge-hay and tussocks etc., needed by the huge nutria population aggregated on the small water sheet of the pond. The shelter material chopped by nutria, covered the bottom as a layer of gritty, organic mud, which decayed and mixed with the mineral ground in 1954, after nutria had been removed and further supply ceased of nesting material.

Destruction of sedge tussocks in the Duzy Lisi bog passed through the same stages as in the fen above the Lesny pond, however, at a quicker pace, owing probably to greater nutria density. The dead tussocks, revealed during the deterioration of the uppermost bog sections, were much smaller than in Lesny pond indicating the more dystrophic character of the habitat. During the winter, the sedge tussocks were hollowed out by nutria as retreats and in search of food. This hastened their depletion.

The sedge destruction and breaking down of the organic layer covering the ground ranged over the terrestrial blanket bog. Pasture grasses and white clover covered the land area denuded of sedges. The pond assumed its initial size and shape in its primeval mineral bed.

Experiment at Stawno, Poland

Description of the site

Stawno Fish Farm located on the flatland between Poznan and Wroclaw is supplied with water by the tributaries of the Barycz River, draining mostly agricultural land. Distrophisation and filling up is much less pronounced there than in Podgorzyn.

In this pond farm the Nowy Swiat Gorny pond which is 25 hectares in area was fenced for nutria breeding. Its water supply is obtained directly from the stream, its outflow going into the Nowy Swiat Dolny pond, it has a constant water flow.

Its plant growth consisted mainly of reeds and cattails. The sedges formed a narrow band along the flat banks. Off the banks their rankness decreased soon. Along the borderline with reeds and cattails the distance between the sedge tussocks exceeded their diameters, unlike the Podgorzyn fens where the sedges formed a continuous front line. The reed stalks pierced the borderline sedge tussocks, also in marked contrast to Podgorzyn, where the reeds were always choked by the encroaching sedges. The isles and the meadow within the enclosure had mineral ground and were overgrown with grass and clumps of alders and pines with raspberry and bilberry undergrowth. The main source of organic matter covering the pond bottom was the decaying reeds and cattails. Their lush growth supplied every year significant quantities of sediment covering the bottom in sheltered spots with thick layers.

Pond development under nutria influence

The pond was stocked in December, 1953 with approximately 1,000 nutria. In the spring of 1954 cattail rhizomes commenced floating up. At first single shreds of the rhizomes (fig. 1) and afterwards small patches appeared on the water surface. The size of floating patches gradually grew, until in June 1954 a crust of several hectares floated up during one night. The high, dead stubble remaining from mechanical mowing in former years also floated up (fig. 2) and formed part of the entire mat. People walked freely on this crust and even shelter building for nutria was started on its

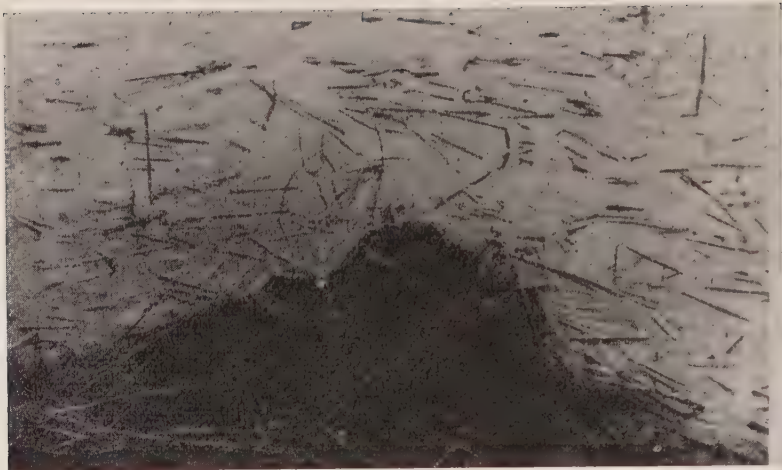


Fig. 1. Shredded weeds around a breeding nest. Nowy Swiat Gorny pond, Stawno, Poland.



Fig. 2. Floating up of a cattail mat caused by nutria cutting. NSG pond.

surface. Cattail shoots and seedlings of various plants appeared on the mat surface. Nutria grazed there constantly. After the young sprouts and shoots had been eaten up, the rhizomes were shredded. In a short space of time nutria were able to dive at any point among the rhizomes and after a month a boat could work its way through the disintegrated crust (fig. 3). During the following months the chopping of the remaining shreds progressed and their bulk diminished until in September the area covered previously by the mat could be passed by boat almost freely. During the deterioration of the floating crust the water was constantly silty, which indicated continuous nutria digging. The mineral silt and nutria droppings doubtless intensified the mineralisation of the vegetative matter shredded and discarded by nutria.



Fig. 3. Disintegration of the cattail mat. Naaman swamps, Israel.

Reed depletion progressed but without any remnants floating up. Within the reed stands nutria browsed mainly on the resprouting shoots until the rhizomes were exhausted and died. Only old stubble remained in the mud (fig. 4).

A distinctive feature of nutria activity at Stawno was breaking of the flat, scarcely emerged, mineral land. Numerous, short trails threading the land among nutria colonies bordering the flat banks changed into water channels, which eventually joined, cutting off sods, resembling sedge tussocks, but of irregular shape. Nutria living in bush clumps and man-made shelters inland cut their way across the meadow until the runs changed into water channels draining the shallow puddles created by nutria digging in the colony area. The constant scouring

of the shores and drainage from the inland puddles enriched the mineral content of water and bottom, stimulating decomposition of organic sediments.

During the spring the growth of duckweeds (*Lemna* sp.), *Stratiotes aloides* and *Salvinia natans* commenced. Later *Lemna* sp. and *S. aloides* waned giving way to *Salvinia* carpet extending gradually upon a large part of water surface. *Salvinia* extended into unsheltered area as dwarfed growth changing gradually into a rank of extremely large plants as the gale was damped.



Fig. 4. Depleted reed stands after draining the pond. NSG pond.

After draining the pond the bottom was denuded of vegetation and the layer of plant debris. Only the old stubble remaining from the previous years' mechanical moving stuck in the thin mud. (fig. 4). Of especial significance seems the deterioration of stalk layers piled by the gale in deep places, where living vegetation (and consequently also the direct nutria activity) was lacking.

Experiment at Kfar Rupin, Israel

Description of the site

The Kfar Rupin Fish Farm is located in the Beth Shean Valley (the southernmost section of the Jordan Valley within the boundaries of Israel), approximately 250 meters below sea level, on slightly alkaline soil and supplied with alkaline water. The locality is con-

sidered warm even for Israel. The ponds receive heavy doses of mineral fertilizers and poultry manure. Under such conditions the reed growth in shallow places is extremely lush. On the other hand decomposition is much more rapid and complete than in the Polish ponds. The swaths of emerged weeds mowed by fish breeders disappear over a period of several months, so that no clogging of water outlet grates occurs and no heap of the plant debris may be found after the drainage of the ponds. Accumulation of the organic matter occurs only under especially favourable conditions.



Fig. 5. Depletion of cattails. Vav pond, Kfar Rupin, Israel.

In the Kfar Rupin Fish Farm two ponds Vav and Shmone, were fenced together for nutria breeding. The larger Vav pond, which is 3.5 hectares in area was overgrown mostly by reed thicket, creeping also on the banks. Cattails bordered the reed stand along the water edge (fig. 5). Within the reed tangle covering approximately 1/3 of the Vav pond a thick layer of dead stalks accumulated. In spots with depth of 0.5 meter or less this layer reached up to the surface. It was so compact that could be walked upon almost without dipping.

Nutria influence on reed layer

The enclosure was stocked with approximately 150, mostly sub-adult nutria in the spring of 1957. The most of them were stocked in the main reed stand in the Vav pond. Afterwards nutria density increased further owing to the aggregation from other colonies and reproduction.

Initially nutria thinned the reeds more or less uniformly. Later barren spots around the feeding tables and extended gradually appeared

(fig. 6). With a decreasing reed area, the rate of depletion grew. During two months the emerged growth was eaten off. Nutria built up their nests on broken stalks (fig. 7) and continued to feed on resprouting shoots. At this time the layer of dead stalks on the bottom shrank considerably, though heavy growth of filamentous algae clinging to the immersed stalks (EHRlich & SPIELBERG 1960) showed that nutria had not yet disturbed this layer. Only after the regrowth of reeds ceased, were the nutria forced to dig out rhizomes. The water became muddy and after draining the pond, its bottom was found denuded of reed layer.



Fig. 6. An eat out in the reeds. Vav pond.



Fig. 7. A nutria nest built on broken stalks. Vav pond.

DISCUSSION

Ecological processes influenced by nutria

The experiments covering a wide range of ponds from dystrophic type in cool foothills of temperate zone, down to the extremely eutrophic pond in the arid and hot depression north of the Dead Sea showed that the organic sediments on the pond bottom, accumulating for years or scores of years disappear in 1—3 seasons under the influence of dense nutria populations.

Nutria realized surprisingly many of the postulates, which may be inferred from investigations of filling up processes. Their feeding on emerged plants is a very efficient method of shredding the coarse water plants postulated by GAJEVSKAJA (1958) which stimulates the disintegration by hydrobionts. Having cut the stalk on or below bottom level, the nutria eats the soft, lowermost parts and unravels the remainder in search for the soft tissue until the discarded part resembles a brush. The volume of the unraveled remainder exceeds many times the eaten part, which accounts for the efficiency of nutria action. The unraveled parts of stalks become very soon densely covered with periphyton and deteriorate. At Kfar Rupin, Israel, the disintegration of stalks unraveled by nutria was continued by turtles which fed on them intensively, unlike the man-mowed stalks, which were never attacked by turtles.

The disintegrating action of nutria is even more pronounced on



Fig. 8. Cutting the reeds and scouring the sedge tussocks. NSG pond.

the rhizomes. Nutria never eat these without carefully peeling them (EHRlich & EINSPOrn, 1956) and discard much more than they eat. The breaking up of the rhizome mat covering the bottom restores the contact between the mineral bottom and the water.

Cutting the emergent stalks renews the contact of the overgrown area with the fertile open water. Scouring the sedge fen by nutria opens it for decay (fig. 8). The aquatic invertebrates and carp continue to disintegrate the dead, decaying tussocks. In this way nutria not only act directly, but initiate a process, carried on by other animals which leads to the complete breakdown of the organic deposits in the fen and the raised bog as well as in the deep swamp.

At the same time drainage is renewed from the land above. Nutria grazing on the terrestrial blanket bogs destroys the dense cover of sedge tussocks and moss cushions thus permitting the development of grasses and white clover, constituting a source of fertile drainage for the ponds. Breaking of the mineral banks by nutria furnishes a further source of mineral silt and other factors stimulating the decay of the organic matter in the water.

Physiological processes peculiar to nutria and turnover in the ponds

In nutria as well as in other rodents the cellulose food is being enriched in proteins and vitamins by fermentation processes occurring in caecum. The biological significance of this process may be indicated by the fact that guinea pigs die if deprived of the reingestion of their faeces (HARDER, 1950). According to the data of HARDER (1950) the caecum of nutria takes 44.0% of the volume of the entire digestive tract, which far exceeds the relative caecum volume of other rodents. As according to HARDER's (1950) results, the part of the food enriched in the caecum corresponds its relative volume, it may be assumed that nearly half of the food ingested by nutria is being enriched in the caecum.

A long list of papers and the fact of bacteria use for vitamin bio-assay show bacteria development, their viability and virility, and even the direction of their action being dependent on vitamin and specific protein supply.

It may be assumed that the enzymatic action of the cellulose digesting caecum fauna may go on and even increase after their discharge in the droppings as there occurs "decharge rapide des substances accumulées par les cellules quand on les replace dans un milieu neuf". (LEFÈVRE, JACOB & NISBET, 1952). Thus, the presence of a dense nutria population in the pond means a constant influx of cellulose decomposing enzymes, which not only directly act upon the

accumulated vegetation, but moreover, probably favor in particular the development of cellulose reducing microflora among the microbes, whose rapid increase in nutria ponds was found by MATUSIAK (1954).

A further factor of rapid microflora increase in the vicinity of nutria colonies found by MATUSIAK (1954) may be afforded by heavy *Salvinia* growth in the investigated ponds. LASARIEV & DOROSINSKI (1953) found in the rhizosphere of water cultures 100—1000 times more bacteria than in the surrounding water. With the increase of the floating plants in nutria ponds their rhizosphere becomes a significant part of the entire biotope, and the materials discharged by their living, dying and sinking, as well as nutria ingested roots may play a role in the microflora increase in nutria ponds found by MATUSIAK (1954) and intensive mineralization of the organic matter stated by the present author.

At last (but not least) the data of LUCAS (1958) suggest the possible significance of hormones, excreted by nutria themselves for the intensity and direction of microflora development in a body of water.

The intensity of nutria action and their influence on the pond development

The intensity of nutria action depends on the population density, the degree of aggregation and the activity of the animals. Thus, no of these factors alone may be the measure of the intensity of the action. The intensity of the action is best expressed by the results observed in the habitat.

The results of a weak nutria activity were observed by ENSMINGER & NICHOLS (1957) in cattail swamps of Louisiana. The cutting of the cattails by nutria was insufficient for the depletion of the stands and produced the regrowth of the cattails. Thus, the amount of plant debris accumulating in the stands haunted by nutria was larger than in the plots unmolested by them, and the processes of filling up were accelerated.

The point of turning the nutria influence from hastening the accumulation of the bottom deposits to the mineralization of the plant matter in the pond seems to be the depletion of the stands of emergent weeds. The depletion of emergent growth forces nutria to dig in the bottom in the search for the rhizomes, thus renewing the contact between the water and the mineral bottom. The manuring becomes a further factor stimulating decomposition. The renewal of the contact with the open water surface enriches the water above the depleted plant bed, removes the products of decomposition and introduces the action of the gale as a further factor of the disintegration of the plant debris.

Owing to nutria preference for deep swamps the whole nutria action and their consequences remain limited to the deep swamp and do not affect the fen as long as the depletion of the emergent vegetation is not accomplished. If the nutria activity becomes stabilized at a level counterbalanced by the regrowth of the emergent vegetation, a balance is established between the choking the water basin by the deep swamp weeds and their mineralization.

The destruction of the fen margins and the reestablishment of the water basin in its primeval mineral bed is being accomplished by a more intense activity of the nutria, which after having depleted the emergent growth, range into the fen and destroy it together with the raised bog, which may develop on the fen's surface.

However, the blanket bog covering the terrestrial grounds is far more resistant to nutria action. Still larger densities and greater activity of nutria is needed to break it down (fig. 8) and reestablish the mineral meadow community above the water body. That changes the nature of the runoff (see the channel on the depleted bog's surface, fig. 9) and increases the trophism. Therefore, the decay within the water body is further stimulated and at the same time the source of the water vegetation able to encroach the pond is removed.

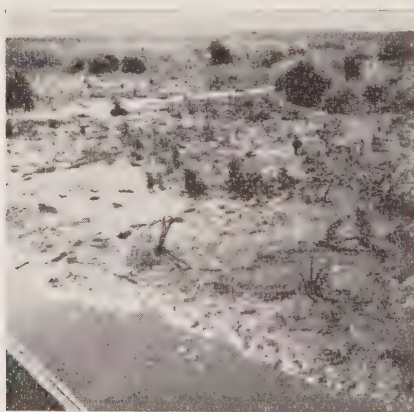


Fig. 9. Depletion of a blanket bog by nutria. Bog lake No 8, Wyszoborz, Koszalin distr., Western Pomorze, Poland.

This type of balance is maintained within a broad range of the intensity of nutria action. The broad scope of this range is due to differences in the behaviour of nutria in relation to land and water plants on the one hand and to the differences in their resistance to nutria grazing on the other. On terrestrial pastures nutria graze only above the ground without digging out the roots (fig. 10). Overgrazed terrestrial ranges are avoided by nutria, which may be due to soiling

by nutria urine or to decrease of nutrient content in the weakened plants, having, — unlike the emergent water plants, — no big nutrient store in its rhizomes. In consequence intensively grazed nutria pastures develop into dense turfs unparalleled by intensively grazed



Fig. 10. Difference between reed depletion in water and on land. Neve Eitan pond, Beth Shean Valley, Israel.

cattle pastures, where trampling overshadows sprouting due to grazing.

With further increase of the density of nutria and of the intensity of their action the depletion of the land vegetation and the erosion of the terrestrial soil commences, at first along the nutria runs. This process is most pronounced on the steep slopes (fig. 11) and on flats slightly emerging above the water level (fig. 9). Climbing on the steep banks destroys the vegetation and pushes down the broken earth. The runs change into deep troughs (fig. 11) which are gradually filled with water (fig. 12). The resulting deep channels are dissecting and undercutting the bank (fig. 13) until it slumps. In this way the steep slope is gradually eroded until it becomes mild and the climbing of nutria ceases to crumble the soil and push it down. Sometimes the same results are produced if a mounting nutria population reverts to burrowing in the abrupt slope with overhanging vegetation. The tunnels collapse and the slumping of the bank continues until the slope degree of the bank becomes too mild for tunnelling.

The water logged soil of the low flats offers also a decreased resistance to the nutria. The runs easily change into channels (fig. 9). Digging and breaking of the soil sets in along the banks of the

newly created channels. The flooded area gains, until the water reaches moderately sloping banks offering better resistance to scouring by nutria. Thus within the activity range exceeding the resistance of the abrupt slopes and the wet flats but insufficient to erode the mild grading slopes nutria act as a factor increasing the water surface.



Fig. 11. Nutria runs troughing the steep banks. Nir David pond farm, Yezreel Valley, Israel.



Fig. 12. Water entering a run changed into channel. Nir David pond.

However, after the wholesale erosion of the banks has set in, the basin is being filled by the soil and the overstocked water body ceases to exist.

Nutria prevent and revert the filling up of the pond only within suitable limits of population activity. Insufficient or excessive activity of nutria acts in the opposite direction, stimulating the filling up.



Fig. 13. Deep channel, dissecting and undercutting a steep bank. Nir David.

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Correlations entre certains caractères synthétiques des populations de phytoplancton

par

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(avec 4 figs.)

INTRODUCTION

L'étude des écosystèmes (écosystème = biocénose + biotope) se trouve engagé dans deux voies différentes. Il y a une tendance strictement quantitative qui fait abstraction des individus et parle en termes de biomasse et productivité, de quantité de matière et de flux d'énergie. D'autre part, persiste l'analyse traditionnelle des populations mixtes naturelles, qui étudie leur composition spécifique, la représentation relative des différentes espèces et les relations spatiales découlant de sa distribution. D'ailleurs, les deux voies d'accès vers la nature, celle du continuum, ou dynamique, et la structurale, ou atomistique, apparaissent conjointement ou alternativement dans toutes les branches de la science.

Une tâche pressante de l'écologie actuelle est d'unifier, d'édifier des ponts entre les deux voies dont nous parlons: d'expliquer certaines propriétés structurelles par les conditions particulières d'un flux d'énergie réalisé ou réalisable, et aussi découvrir la mesure dans laquelle le flux est contrôlé par la structure de la population traversée. Cette tâche pose des questions préliminaires. Une d'elles est trouver des expressions quantitatives simplifiées des propriétés structurelles. Si on ne dispose pas d'elles, la tâche de mettre en rapport la structure, la biomasse et le flux d'énergie, risque de s'égarer dans des constructions rhétoriques.

Le but de cette note est d'examiner quelques propriétés synthétiques des populations de plancton qui peuvent exprimer d'une

façon simple et donnent une assez bonne idée de la structure. Le phytoplancton marin de Castellón, dans la Méditerranée occidentale, a été utilisé comme matériel servant de base à ces considérations. Dans une autre publication (MARGALEF & HERRERA, sous presse) on trouvera des tables détaillées de la composition spécifique des échantillons de plancton, de la concentration des différents pigments végétaux et, enfin, des caractéristiques physiques et chimiques du milieu marin. Ces données ont servi pour le calcul des chiffres qui figurent sur le tableau I.

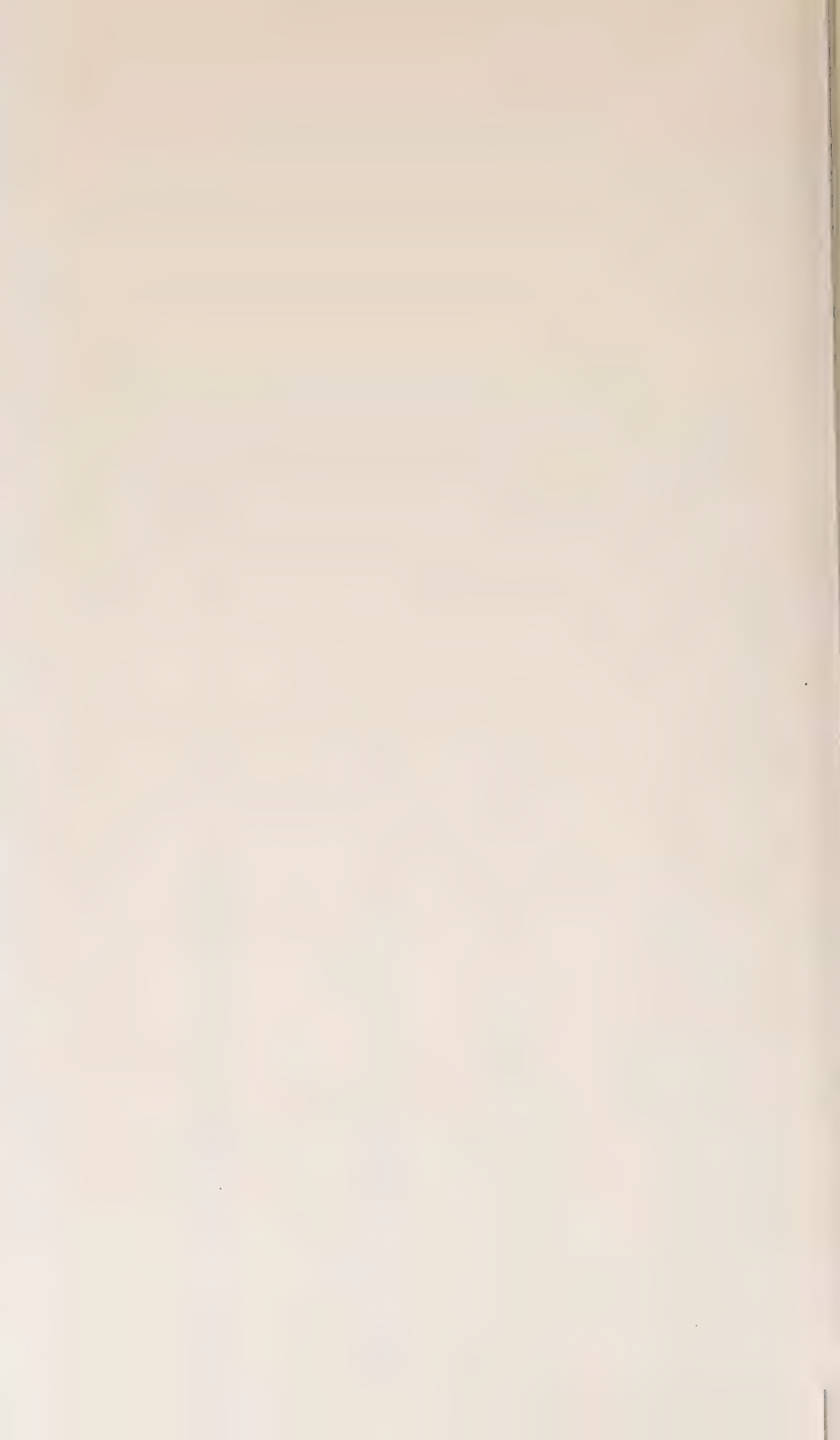
Le matériel n'est pas tout à fait approprié. Les échantillons étudiés qualitativement et quantitativement sont le résultat de pêches faites au filet fin (70 fils par cm) en surface. La sélection du filet représente une simplification et une distortion de la structure de la communauté réelle. Ces mêmes échantillons ont servi pour calculer le rapport entre nombre total de cellules et nombre de cellules de dino-flagellés. En général, le nombre de cellules identifiées dans chaque échantillon était seulement de 200 à 500. Les concentrations de chlorophylle *a* se rapportent à des échantillons d'eau superficielle pris en même temps. Le quotient D_{430}/D_{665} représente le rapport entre les densités optiques à 430 et 665 millimicrons d'un extrait acétonique du phytoplancton (MARGALEF, 1960); les valeurs supérieures à 6 doivent s'attribuer à la présence de considérables quantités de caroténoïdes de procédence animale simultanément à des concentrations très basses de chlorophylle. Puisque les valeurs de D_{430}/D_{665} sont souvent erratiques en surface par une majeure fréquence de caroténoïdes étrangers au phytoplancton, on a computed les valeurs qui figurent dans la colonne (8) du tableau I en prenant les moyennes des valeurs trouvés à différents profondeurs pour la station et la date indiquées.

DIVERSITÉ SPECIFIQUE

On peut mesurer la diversité d'un ensemble de N éléments appartenant à S catégories différentes par le nombre de combinaisons qu'on peut réaliser avec cet ensemble: $\frac{N!}{N_a!N_b!\dots N_s!}$, où N est le nombre total d'éléments (dans notre cas d'individus) et N_a, N_b, \dots, N_s , sont les nombres d'éléments appartenant aux catégories a, b, \dots, s (dans notre cas, le nombre d'individus de chacune des S espèces). (MARGALEF, 1957). L'expression

$$I = \frac{N}{1} \log_2 \frac{N!}{N_a!N_b!\dots N_s!} \quad (1)$$

donne la diversité d'un ensemble en bits par individu.



Cette expression semble assez appropriée, mais demande l'énumération des individus de chacune des espèces et la computation n'est pas toujours aisée. D'autres indices de diversité proposés étaient plus faciles à calculer. Le plus connu est celui de FISHER, CORBET & WILLIAMS (1943). Ces indices plus simples se basent sur une intéressante propriété des assemblages naturels d'individus appartenant à différentes espèces, qui se manifeste en ce que les valeurs $N_a, N_b, \dots N_s$, montrent une certaine régularité, de façon qu'on peut les remplacer, sans trop d'erreur, par une série logarithmique. Si on suppose que quand le nombre d'individus croît suivant une progression géométrique, le nombre d'espèces croît suivant une progression arithmétique, ce qui n'est pas loin de la réalité dans nombre des populations mixtes, on arrive au plus simple des indices de diversité

$$d = (S - 1) / \log_e N \quad (2)$$

Si les populations réelles s'accordent à l'hypothèse qui sert de base à l'index de diversité employé, on doit s'attendre trouver une corrélation ou correspondance parfaite entre l'index alpha de FISHER, CORBET & WILLIAMS, ou d , par exemple, et I . Il va sans dire que la régression ne sera pas linéale. Un éventuel départ entre les indices I et les indices plus simples nous donnera une mesure du degré de l'écart entre la distribution des individus en espèces au sein de la population réelle et la distribution hypothétique qui sert de base à l'index utilisé.

Théoriquement, un index de diversité ne doit changer avec l'augmentation de l'échantillon si celui-ci est tiré d'une population homogène. Dans la pratique, l'indice augmente au début, à mesure qu'augmente le nombre d'individus recensés, puis atteint un „plancher” où, néanmoins, il y a toujours une augmentation très lente. Le problème posé implique dans ce point demande une préalable clarification de ce qu'on doit concevoir comme homogénéité, par rapport à une structure qui s'étend indéfiniment dans l'espace.

TABLEAU II

Coefficients de corrélation entre les indices de diversité I et d , d'après les données du tableau I. Dans tous le cas, la probabilité que la corrélation trouvée soit due au hasard est inférieure à 0.001.

| | Dinoflagellés | Diatomées | Total |
|-----------------|---------------|-----------|-------|
| Station A | 0,97 | 0,84 | 0,66 |
| Station B (+ C) | 0,88 | 0,87 | 0,67 |
| Toutes stations | 0,92 | 0,86 | 0,67 |

Les corrélations entre d et I , calculées sur les chiffres du tableau sont présentées sur le tableau II. La conclusion qui s'en dégage confirme celle présentée avec un matériel différent et plus restreint dans des publications antérieures (MARGALEF, 1957): le simple indice $d = (S - 1)/\log_e N$, si facile à calculer, fournit une estimation assez bonne de la diversité appréciée par des méthodes plus exactes.

On a calculé séparément les indices de diversité et les corrélations pour la partie de la population formée par les diatomées et par les dinoflagellés, comme éléments principaux du phytoplancton étudié. La corrélation entre les deux indices est plus forte dans les populations de dinoflagellés que dans celles de diatomées. La régression qui relie les deux indices est aussi différente (Fig. 1) dans les deux cas. Il est vraisemblable que l'aggrégation fréquente des cellules de diatomées en colonies, ainsi que la dynamique plus intense de certaines populations, donnent à celles-ci des propriétés structurales un peu différentes.

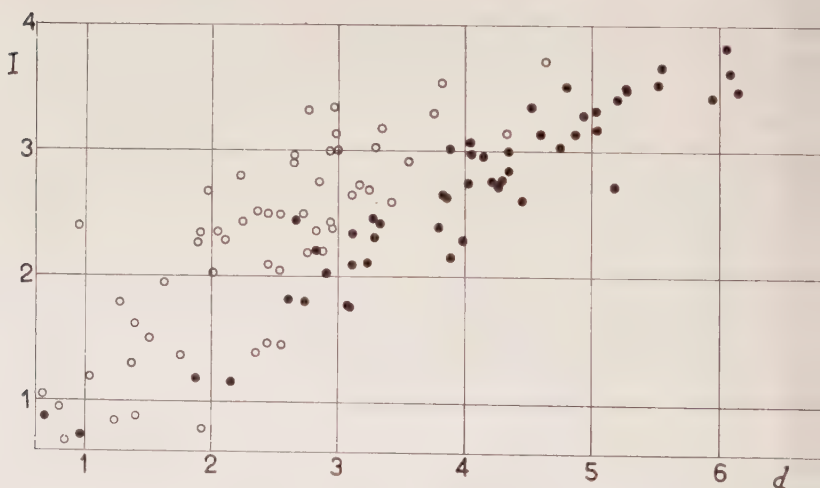


Fig. 1. — Indices de diversité d (en abscisses, $d = (S - 1)/\log_e N$) et I (en ordonnées, $I = \frac{1}{N} \log_2 \frac{N!}{N_a! N_b! N_s!}$) des populations de diatomées (cercles blancs) et de dinoflagellés (cercles noirs). A remarquer que la correspondance entre les deux indices de diversité considérés varie suivant le groupement taxonomique.

DIVERSITÉ DES PIGMENTS

Dans le phytoplancton on reconnaît un nombre considérable de pigments qui interviennent dans la photosynthèse. Les proportions relatives des différents pigments varient avec une certaine régularité.

On peut dire, par exemple, que quand on trouve une participation forte de chlorophylle b, on doit s'attendre à trouver une concentration également élevée de caroténoïdes astaciens et une concentration encore plus forte de chlorophylle c. Ceci rappelle la tendance observée dans la participation des différentes espèces dans la communauté, dont la régularité permettait l'utilisation d'indices de diversité très simples. On peut parler, aussi, d'une diversité par rapport aux pigments. Dans le cas de diversité minimum, on aura une forte proportion de chlorophylle a et des faibles quantités de caroténoïdes; la diversité maximum est réalisée quand la proportion relative de chlorophylle a est basse par rapport à la quantité totale des pigments, et ceux ci son nombreux, qualitative et quantitativement.

L'étude précis se heurte à maintes difficultés. Le procédé habituel de computer les concentrations d'un certain nombre de pigments ou de groupes de pigments en partant des spectres d'absorption des extrait de plancton, contient de nombreux éléments d'imprécision. Seulement une étude chromatographique soignée pourrait fournir des données exactes. De toute façon, si on désire seulement avoir une idée approximée de la diversité des pigments, on peut trouver des expressions bien plus simples et que, vraisemblablement, ne sont pas pires dans son domaine que les index de diversité spécifique, comme d. L'index D_{430}/D_{665} , qui est le quotient entre les densités optiques aux longueurs d'onde de 430 et 665 millimicrons des extraits acétoniques du phytoplancton, fournit des valeurs qui semblent appropriées. Il est bas dans les populations simples, à croissance rapide, avec une proportion excessive de chlorophylle a; il monte graduellement dans les populations plus âgées ou plus complexes, dont la diversité des pigments est grande.

On a employé cet index auparavant (MARGALEF 1960), d'une façon empirique, pour caractériser les populations de phytoplancton, mais il est bon remarquer qu'on peut le considérer comme une expression de la diversité des pigments.

RAPPORTS ENTRE DIVERSITÉ SPÉCIFIQUE ET DIVERSITÉ DES PIGMENTS

Si on se souvient que les échantillons qui ont servi pour les obtenir ne sont pas exactement les mêmes, on peut qualifier de bonne la corrélation entre la diversité spécifique et la diversité des pigments, $+0,405$, avec une probabilité prochaine à 0,001 d'être attribuable au hasard. Dans nombre de phénomènes écologiques, l'emploi de corrélations entre des valeurs simultanées n'est parfois complètement satisfaisant. La considération dynamique des phénomènes, la projection dans le temps des changes des diversités (fig. 3) confirme

la réalité de la corrélation que nous sommes en train de considérer.

La pensée la plus constructive qui s'en dégage est, peut être, l'acceptation de la possibilité de projeter sur des différents niveaux la structure d'une biocénose, par d'autantes opérations intellectuelles. La distinction en individus, la classification des individus en espèces, nous porte à parler d'une structure dont une expression simplifiée est l'index de diversité spécifique. La distinction en systèmes photo-synthétisateurs, en quelque sorte symbolisés ou représentés par des différents pigments, nous conduira à exprimer une structure, pré-supposant sa cohérence ou régularité, par un index de diversité des pigments. Ce qui est plus important: sur les deux plans se reflètent, d'une façon pareille, certaines propriétés (dynamiques) basiques des populations, du flux d'énergie qui traverse les populations. Il est bon insister que la distribution en individus et en espèces est seulement un des aspects structuraux d'une population mixte naturelle et, peut être, pas même le plus important.

AUTRES CORRÉLATIONS

Dans des travaux antérieurs se rapportant au plancton au large de Castellón, on avait trouvé une corrélation acceptable entre la concentration de pigments, exprimés en unités Harvey (UPH) et la masse totale du phytoplancton par rapport à la masse des dinoflagellés. Maintenant on a calculé la corrélation entre concentration de chlorophylle a et rapport entre nombre total de cellules et nombre de cellules de dinoflagellés. Le coefficient de corrélation (+ 0,122 pour 54 paires de valeur) n'est pas significatif. Néanmoins, la projection dans le temps des deux phénomènes (fig. 4) montre qu'il y a une correspondance indéniable.

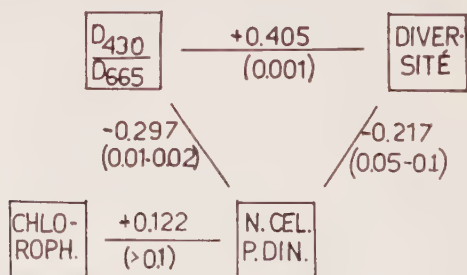


Fig. 2. — Corrélations entre différents caractères synthétiques des populations de phytoplancton: Index de diversité (I), quotient D_{430}/D_{665} , nombre total de cellules pour chaque cellule de dinoflagellé et concentration de chlorophylle a. Au dessous de la corrélation, entre parenthèses, se donne la signification du coefficient de corrélation (probabilité que la corrélation trouvée soit due au hasard).

Le rapport: nombre total de cellules/nombre de cellules de dinoflagellés montre une corrélation négative faible avec l'index de diversité spécifique et le quotient D_{430}/D_{665} (fig. 2). A ce sujet aussi, la comparaison de l'évolution des populations (figs. 3 et 4) conduit à l'esprit la conviction d'une correspondance bien plus forte de celle qui se reflète dans les coefficients de corrélation.

RAPPORTS DYNAMIQUES ENTRE LES DIFFÉRENTS CARACTÈRES SYNTHÉTIQUES ÉTUDIÉS

Il me semble que les correspondances deviennent bien claires et significatives quand on place le problème de la structure sur le fil de la succession écologique. Dans la période étudiée, quatre successions se suivent, toutes commencées par un enrichissement de l'eau en phosphate, qui joue le rôle de facteur limitant principal dans nos eaux. Les dates du début des successions respectives sont: Juin 1959, Novembre-Décembre 1959, Février-Mars 1960 et Juin 1960. Chacune de ces successions a ses caractéristiques biotiques particulières, mais toutes montrent un fort parallélisme dans le développement des propriétés exprimées par les chiffres du tableau I. On peut dire que cette façon de considérer les structures permet de s'élever au dessus de la tâche de l'identification des espèces, et saisir des généralisations d'un certain intérêt.

Des études expérimentales en cultures complètent l'image de la succession. Si nous partons d'une culture mélangée et âgée, à index de diversité élevée et quotient D_{430}/D_{665} haut et faisons possible une augmentation de la productivité, la rapide multiplication de certaines espèces et la rapide synthèse de chlorophylle a font tomber, à la fois, la diversité spécifique et la diversité des pigments. La même chose se passe dans les populations naturelles, accompagnée d'une élévation de la concentration de la chlorophylle a et de la participation relative des diatomées. L'allure parallèle et régulière des graphiques 3 et 4 le démontre bien. Plus tard, la diversité monte, la composition pigmentaire se complique, la concentration de chlorophylle a tombé et la participation relative des dinoflagellés devient plus forte, jusqu'à l'initiation d'une nouvelle succession.

Suivant ces considérations on pourrait trouver le trait d'union qui nous intéresse entre flux d'énergie et structure, mais un examen détaillé de ces questions demanderait être en possession de plus de données positives, tant d'observations dans la nature comme dans des cultures de laboratoire.

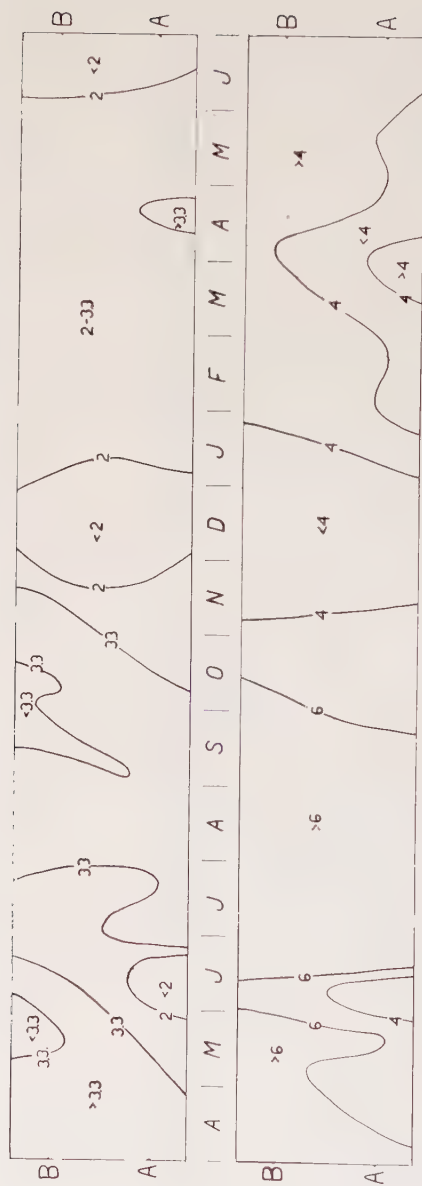


Fig. 3. — Distribution de l'index de diversité (I , partie supérieure) et du quotient D_{430}/D_{665} (partie inférieure) dans les stations A et B du mois d'Avril de 1959 au Juin de 1960. Entre les stations A et B il y a 8 milles, la B se trouvant plus au large.

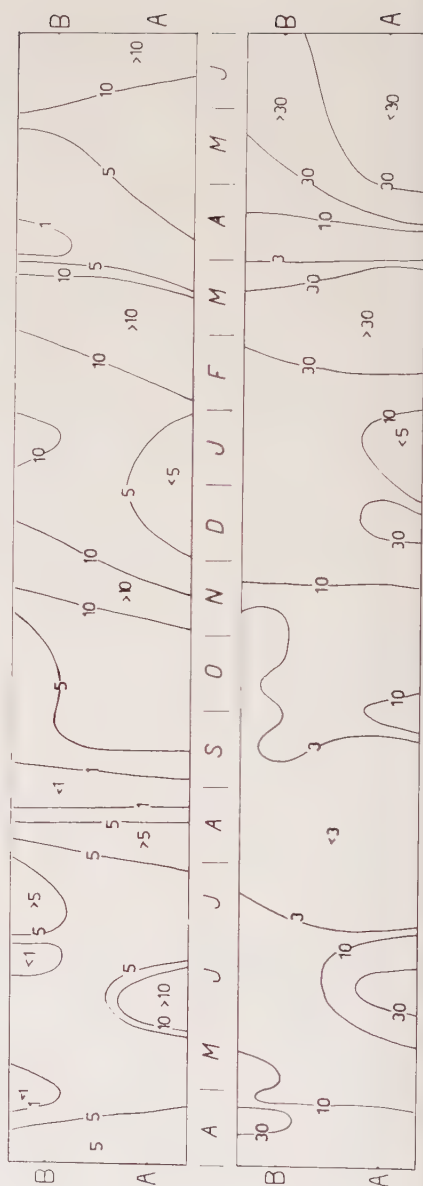


Fig. 4. — Distribution de la concentration de chlorophylle *a* (en $\mu\text{g par } 100 \text{ l}$ partie supériorisée) et du moment

RÉSUMÉ

Du point de vue de la structure, les populations de phytoplancton peuvent être décomposées en différents éléments: individus, systèmes photosynthétisateurs, etc. Les indices de diversité biotique fournissent une mesure de certaines propriétés structurelles quand les individus sont les éléments de la structure. Quelques indices simples tirés des spectres d'absorption des extraits du phytoplancton (par exemple, D_{430}/D_{665}) donnent une estimation de propriétés structurelles quand les systèmes photosynthétisateurs sont pris comme les éléments de la structure. Des observations faites sur le plancton de la Méditerranée, au large de Castellón, donnent une corrélation positive entre la diversité biotique et le quotient D_{430}/D_{665} , qui peut être considéré comme un indice de diversité des pigments. Cette corrélation demande une interprétation dynamique. Quand les conditions du milieu permettent une poussée dans la production, se manifestent les conséquences de l'inégalité des taux de maximum d'accroissement parmi les éléments de la structure en concurrence (espèces ou pigments) et les indices de diversité deviennent plus petits. Le même phénomène, qui suppose des relations étroites entre le flux d'énergie et la structure, facilite l'explication d'autres corrélations moins importantes entre caractères du phytoplancton.

SUMMARY

The structure of phytoplankton populations may be assessed at different levels: in terms of individuals, of photosynthetic systems, and so on. Biotic diversity gives a measure of certain structural properties when individuals are considered as the pieces of the structure. Some simple ratios computed on the absorption spectra of phytoplankton extracts (i.e., D_{430}/D_{665}) give a measure of structural properties when photosynthetic systems are considered as the pieces of the structure. Observations made in the Mediterranean, off Castellón, show a positive correlation between biotic diversity and index D_{430}/D_{665} , that can be considered as an index of "pigment diversity". Such correlation can be understood with dynamic approach. When environmental conditions become adequate for a push in the production, the inequality of the maximum rates of increase for the different pieces of the structure (species or pigments) leads to a decrease in the diversity (biotic diversity and index D_{430}/D_{665}). The same phenomenon helps explain other less noteworthy correlations.

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Growth of *Tilapia mossambica* Peters in Some Transvaal Impoundments

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(with 8 figs.)

INTRODUCTION

Since *Tilapia mossambica* is an important sporting fish in the Transvaal, it was necessary to find a way of determining its growth rate to facilitate intelligent management. Although GARROD (1), HOLDEN (2) and others had difficulty in using the scales of *Tilapia* for age determination in the tropics, it was thought that the temperate waters of Transvaal would make them easier to interpret.

Since the larger irrigation impoundments of the province provide most of the fishing, especially in urban areas, this study was confined to the fish of such dams.

METHODS

Scales were collected during routine surveys of dams, sorted, cleaned and dry-mounted. The samples were taken from the pectoral region below the lateral line of the fish. Measurements of the scales were taken to the nearest .05 millimeter with the aid of a home-built projector and fish were measured for total length in inches — either decimals or fractions being used.

All calculations were made by slide rule.

TIME OF FORMATION OF THE RINGS

It was immediately apparent that regular breaks or rings could be detected in the anterior part of the scales from most localities. (Fig. 1).

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These rings were formed anteriorly by a slight break in the regular pattern of the circuli and towards the sides of the scale by the overlapping of a complete circulus over a number of incomplete ones (Fig. 2).

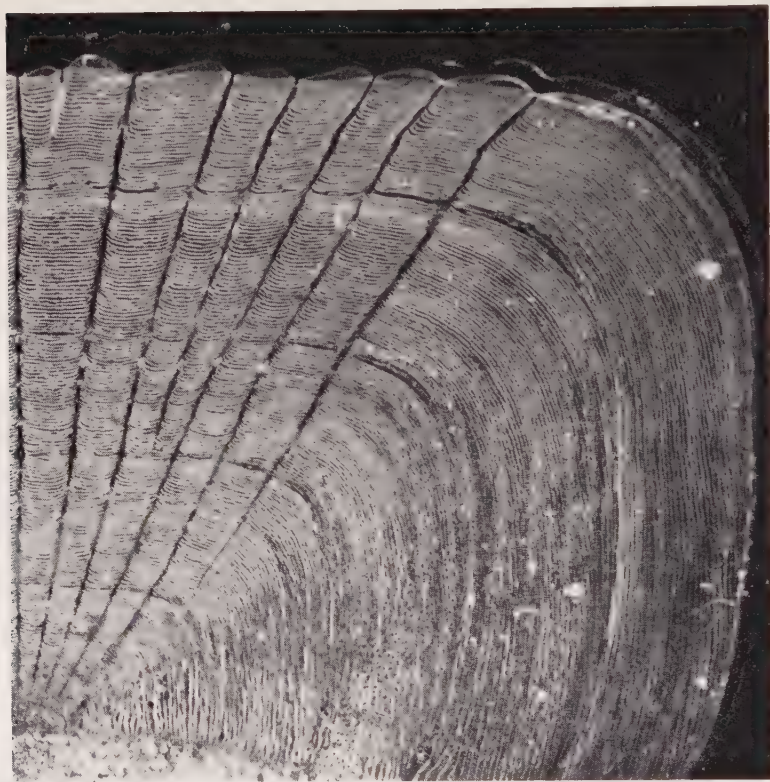


Fig. 1. Anterior field of scale showing regular ring formation - No. S 220 B.

The regularity of occurrence of these rings suggested that a rhythmical seasonal process was responsible for their formation.

Marked fish kept at the Provincial Fisheries Institute, Lydenburg, under normal hatchery conditions regularly showed one mark after one year (Fig. 3) and as *T. mossambica* breeds at this age, the ring could either be formed by spawning activity or as a result of the rather severe winter at this station.

As the body-length showed a straight-line relationship with the shortest anterior radius of the scale, at least in fish over three inches long, the simple formula $\frac{\text{Distance from focus to ring}}{\text{Anterior radius of scale}} \times \text{Length of}$

fish when caught = Length of fish at time of ring formation was used to determine the length of the fish at the time of formation of any ring noticed.

Using this formula, the calculated length of the fish at the time of formation of the ring put the period of formation somewhere about the end of winter, which in the Transvaal is August.

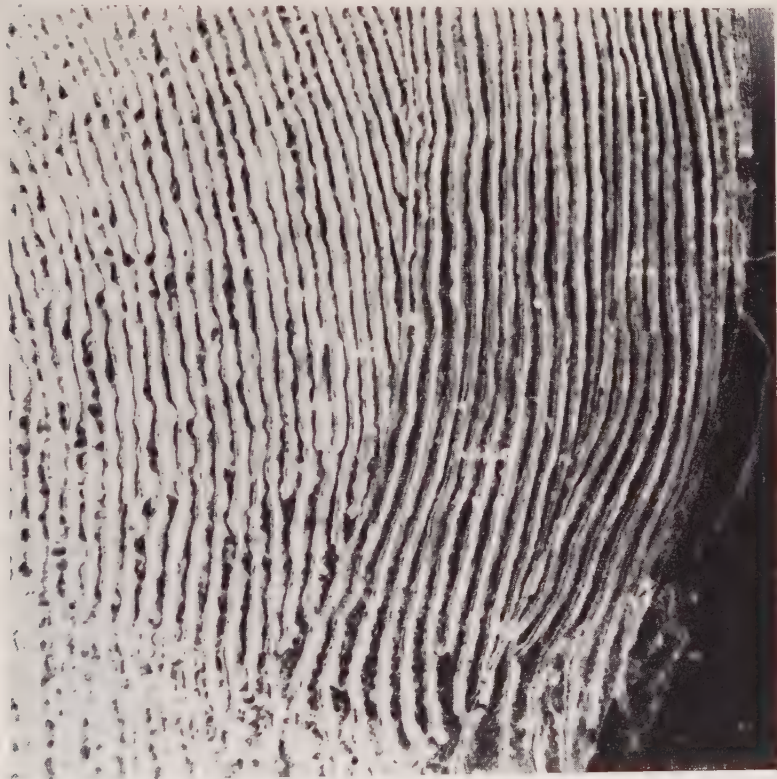


Fig. 2. "Cutting over" of circuli in region between exposed and unexposed parts of scale. - No S 39 B.

Nearly all of the dams from which samples were collected in this survey are subjected to a relatively severe winter for *Tilapia*. During these periods the fish are not only inactive, but heavy mortalities sometimes occur in some dams in the southern part of the province. (All dams are situated at about 4,000 feet above sea level.)

This, together with the fact that gonad development takes place during the latter part of winter and early summer may account for the resorption, which, as WALLIN (3) pointed out, starts at the boundary between the exposed and unexposed parts of the scale. This also

accounts for the observation that 'cutting over' is usually most noticeable in this part of the scale.

In hatchery fish older than one year it was difficult to interpret the rings because it seemed as if handling, transfer from one pond to another, etc., could induce the formation of some sort of break. Thus fig. 4 shows the distorted kind of broken up area formed when a fish was transferred from one pond to another immediately after spawning, as contrasted to the clear breaks formed under natural conditions (Figs. 1, 2 and 5).

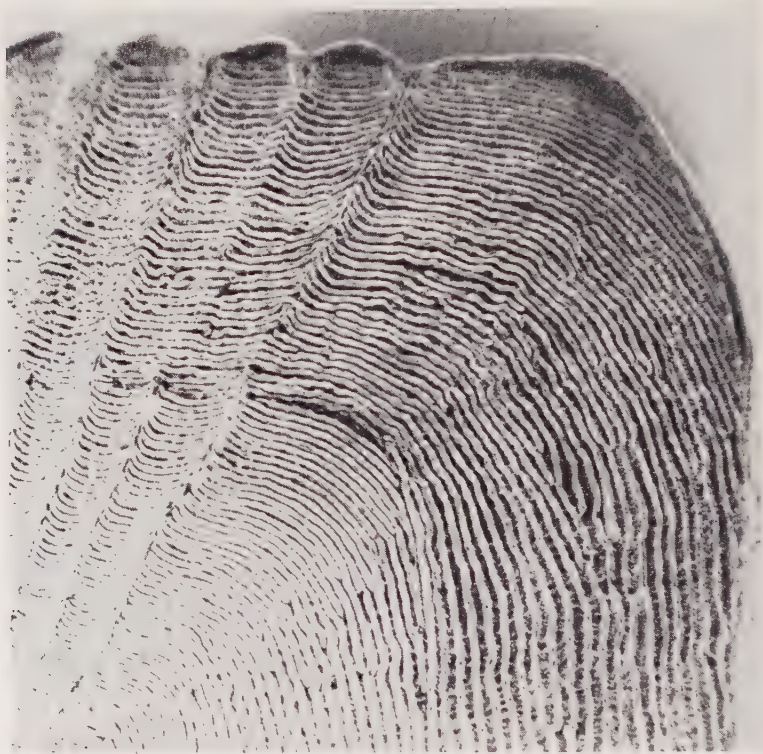


Fig. 3. Scale of hatchery fish, one year old showing one annulus. - No. 581 L.

Confirmation for the hypothesis that the rings were formed in winter, (June to August), was found in certain samples of scales collected during the middle of August, which showed a ring being formed on the very edge of the scale or just inside it (Fig. 5).

Further confirmation was found in the length-frequency distribution of a large sample of fish collected from one of the dams in this survey, the Njelele Dam. If it is assumed that *Tilapia* do not grow during the two coldest months (June and July), then the modal size

frequencies of fish collected from this dam in February 1960, as shown in GROENEWALD's (4) work on the dam fit in very well with the sizes of the fish as calculated from the rings on the scales, assuming that they were formed in August, i.e. some four months of active growth after GROENEWALD's date of collection. The data are given in Table I.

TABLE I

| Length \ Age | 0 + | I + | II + | III + |
|------------------------|----------|---------|---------|---------|
| Actual (in February) | 1.2—1.95 | 5.1—5.5 | 7.9—8.2 | 9.5—9.8 |
| Calculated (in August) | 4.8 | 7.1 | 8.5 | 9.5 |

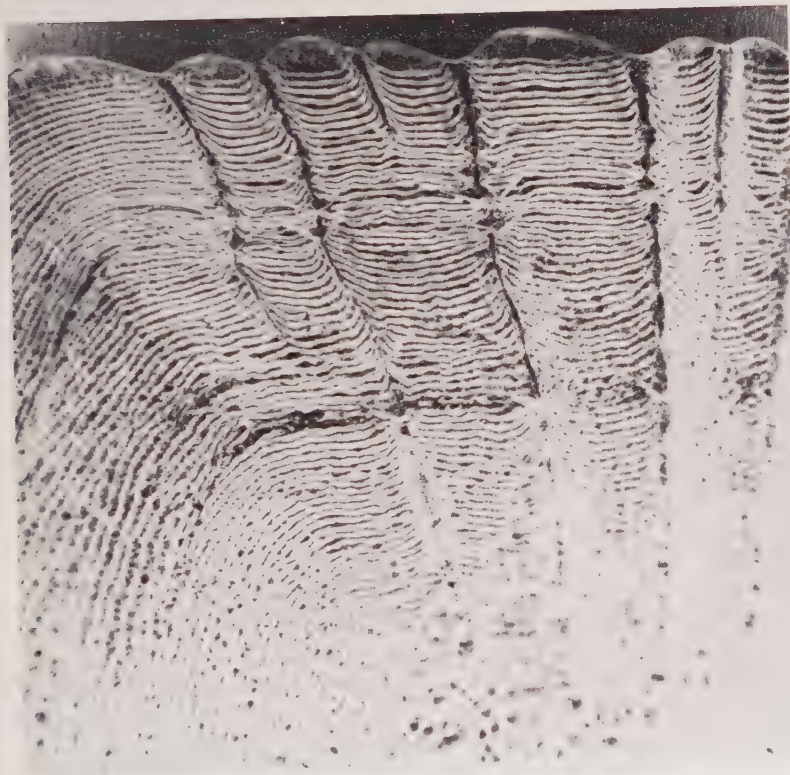


Fig. 4. Scale of hatchery fish showing distorted growth and false marks. - No. 577 R.

If the actual lengths are interpolated on the growth curve (Fig. 7) making due allowance for the time of collection, a remarkably close fit is obtained.

It was therefore concluded that the rings seen on the scales of *T. mossambica* could be interpreted as annual marks formed during late winter or early summer and August was regarded as the most probable month of formation of the annuli.

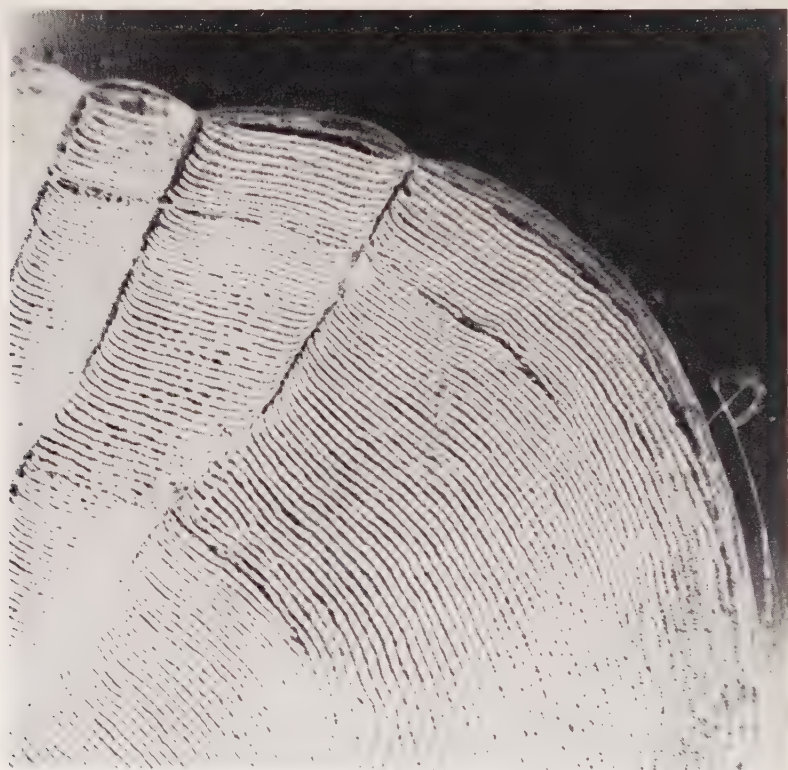


Fig. 5. Annulus being formed on scale edge. - No. 658 M.

VARIATIONS IN GROWTH RATE IN DIFFERENT DAMS

Growth rate varied widely in different waters (compare Figures 1 and 6) so that even a small sample from an individual dam was considered as an entity and a separate curve calculated for it.

The data are presented graphically in figures 7 and 8 and the peculiarities of each curve are only discussed shortly.

The great range of lengths especially at earlier ages is attributed

to the long spawning season. Thus some spawning activity may be found from October to April, and even later in the warmer parts.

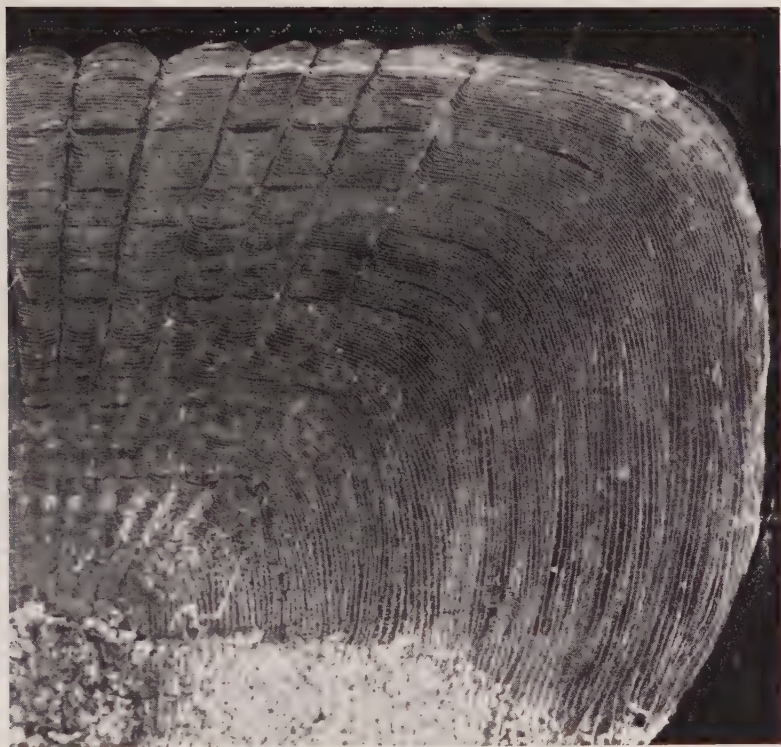


Fig. 6. Numerous annuli on scale of II-inch fish from Lake Fundudzi - 496 L.

NJELELE DAM (Fig. 7)

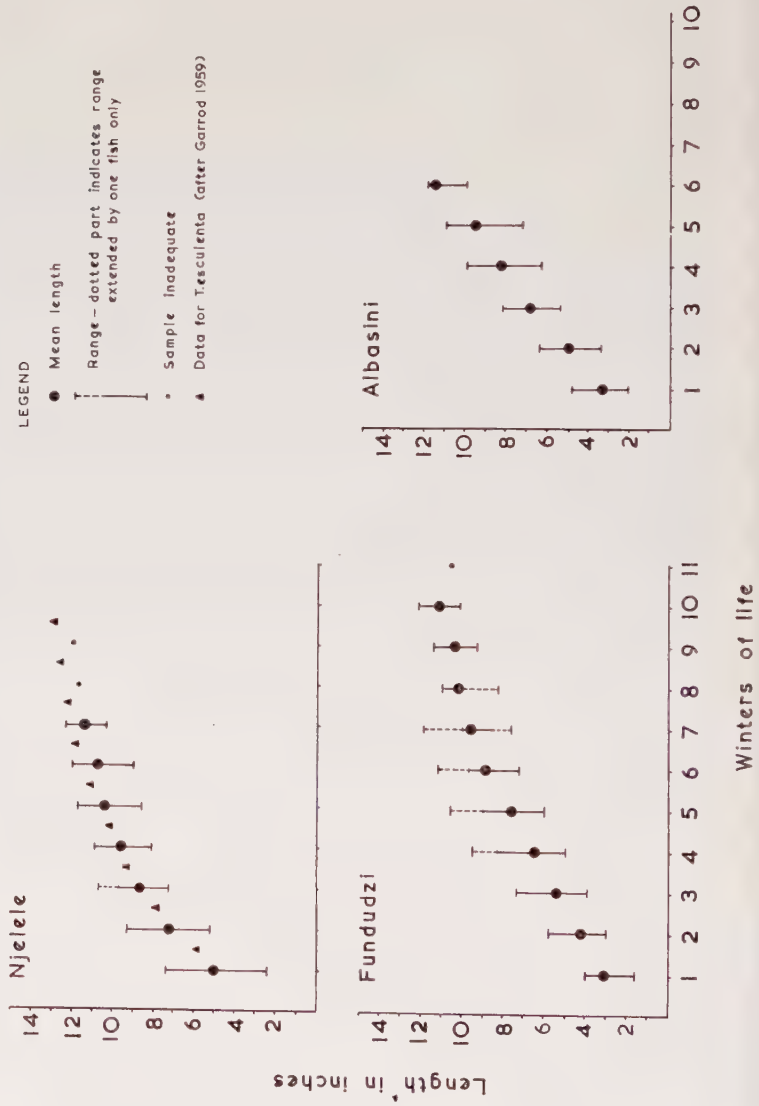
Locality $30^{\circ}7'E$ — $22^{\circ}44'S$.

Size of sample — 64 fish.

This is the most northerly of the dams sampled and the growth curve indicates good growth during the first two summers, after which it falls off. As found by GARROD (op cit.) for *T. esculenta* in Lake Victoria, the fish seem to be fully grown in length at ten years. Only in Fundudzi Lake were fish found that indicated an age of eleven years (Fig. 7).

If the spawning period is taken to fall between two successive annuli there is a great similarity between the growth of the *Tilapia mossambica* in this dam and that of *T. esculenta* in Lake Victoria. If GARROD's data for the growth of *T. esculenta* in the Jinja area are

Fig. 7 CALCULATED GROWTH CURVES FOR *T. MOSSAMBICA*



compared with that of *T. mossambica* as in fig. 7, there is less variation between the two curves than between GARROD's curves for fish from various localities in Lake Victoria. (Measurements were taken from the published graph in GARROD's work and not from the original figures.)

FUNDUDZI LAKE. (Fig. 7)

Locality $30^{\circ}20'E - 22^{\circ}50'S$.

Size of sample — 25 fish.

Angler's reports and a routine survey of this natural lake indicated that it is heavily overpopulated. The growth curve confirms this and growth is by far the slowest of all the dams sampled. Very few scales were available for the calculation of the older age groups since the scales from older fish were as a rule very dense and the annuli difficult to distinguish because of their number. One of the clearer scales is reproduced as fig. 6.

ALBASINI DAM. (Fig. 7)

Locality $30^{\circ}6'E - 23^{\circ}6'S$.

Size of samples — 15 fish.

Only three fish of more than five years old were sampled and all three were apparently exceptionally fast growing specimens so that the mean for the sixth annulus falls considerably above the expected value. Judging by the first five years the average growth rate is considerably less than that of Njelele, mainly as a result of the much slower first and second year growth.

LOSKOP DAM. (Fig. 8)

Locality $29^{\circ}21'E - 25^{\circ}25'S$.

Size of sample — 27 fish.

Fish are reported to be scarce in this dam but good specimens are regularly taken. The growth curve supports this and the growth of fish older than two years is much faster than that of the more northerly dams.

RUST-DER-WINTER DAM. (Fig. 8)

Locality $28^{\circ}28'E - 25^{\circ}14'S$.

Size of sample — 18 fish.

Much the same type of growth as Loskop. Unfortunately no fish older than five years were available.

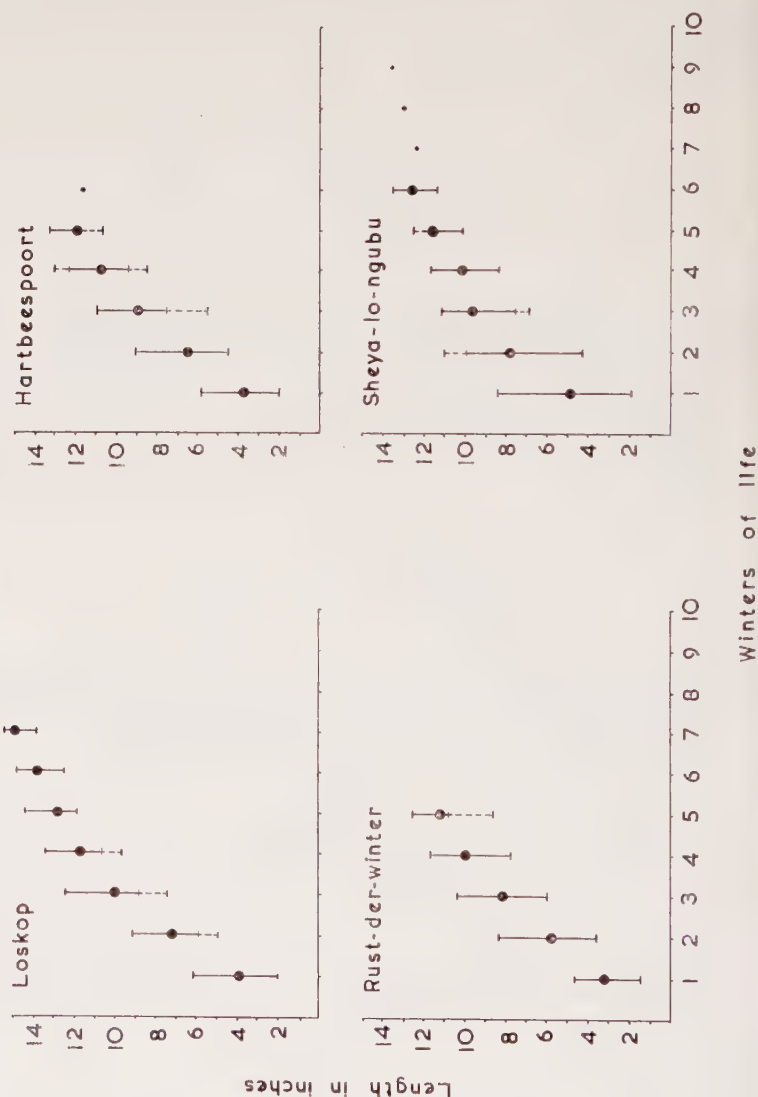
HARTBEESPOORT DAM. (Fig. 8)

Locality 27°50'E — 25°44'S.

Size of sample — 35 fish.

This dam is subjected to the heaviest fishing pressure in the Transvaal and thousands of good fish are annually taken. In addition to that, winter mortalities of *Tilapia* is a common occurrence.

Fig. 8 CALCULATED GROWTH CURVES FOR *T. MOSSAMBICA*



Growth seems to be the same as in Loskop and again no fish older than five years were caught.

S H E Y A - L O - N G U B U D A M. (Fig. 8)

Locality 31°20'E — 25°43'S.

Size of sample — 12 fish.

This is one of the most southerly of the dams carrying *Tilapia* in the province and the only one which carries Black Bass (*Micropterus salmoides*) as well. Growth is good, especially during the first two years but falls off rather sharply from the third year onwards when compared to the other southerly dams.

In general it would seem that the fish in the more southerly dams have a better growth rate than those in the dams of the warmer Northern Transvaal. The reason for this is not known but it is not considered to be connected with latitude or water temperatures but rather with factors like water fertility and population density.

S U M M A R Y

1. Scales of *Tilapia mossambica* from six large irrigation impoundments and one natural lake in Transvaal were used to determine the growth rates of the fish.
2. Regular rings on the scales are laid down annually at the end of winter. This conclusion is supported in the case of one impoundment by a study of length-frequency distribution.
3. Growth of *T. mossambica* apparently stops during the two coldest months, June and July, and this promotes the formation of regular annuli.

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P. VAN OYE

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